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## A Qualitative Analysis of Differential Equations of Population Dynamics

Kevin Brenner

*College of Saint Benedict/Saint John's University*

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A Qualitative Analysis  
of  
Differential Equations  
of  
Population Dynamics

A THESIS  
The Honors Program  
College of St. Benedict/St. John's University

In Partial Fulfillment  
of the Requirements for the distinction "All College Honors"  
and the Degree Bachelor of Arts  
In the Department of Mathematics

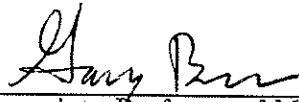
by  
Kevin Brenner  
May 1, 1994



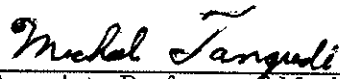
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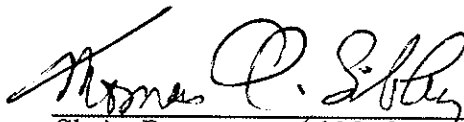
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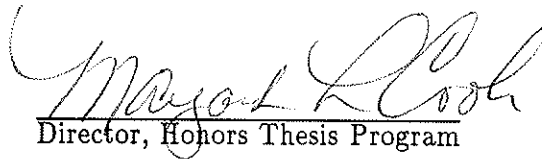
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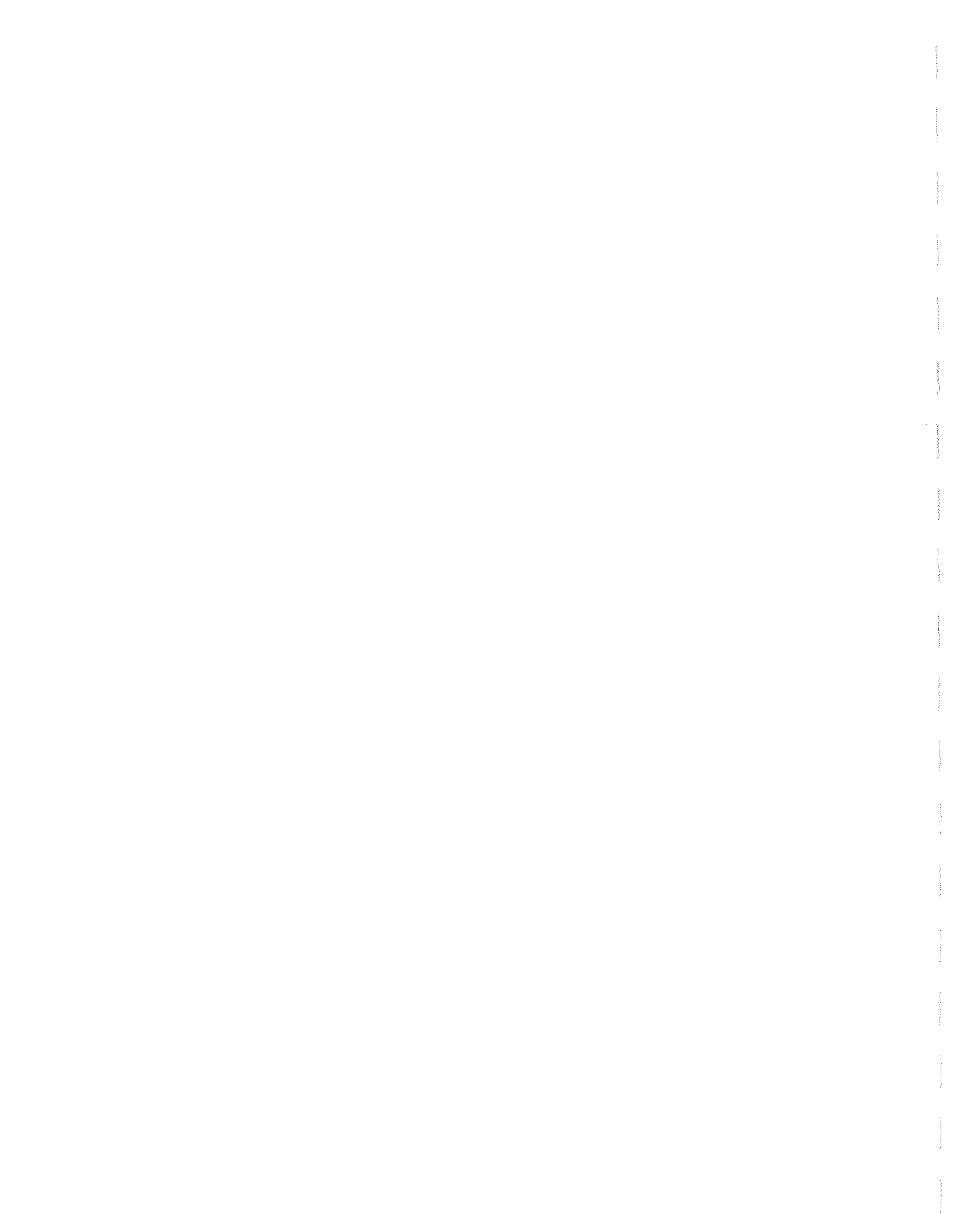
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This work is a qualitative analysis of differential equations. The systems of differential equations studied in this work are models for systems which could naturally occur between species in the environment. Each model is made by adapting to characteristics observed in natural ecosystems. These adaptations are the assumptions of the model.

The models discussed in this work are only hypothetical. While it is possible to include a small number of the most important characteristics of an ecosystem in the model, every characteristic cannot be included. Thus, models can give us a general idea of how the populations will behave, but do not exactly describe a population.

To simplify the analysis, the hypothetical models in this work are all closed. In a closed model the migration of species is not possible. Also, no new species can enter a closed model. Another characteristic of the closed models is a constant environment. This removes the factors of seasonal change, severe weather, and other natural catastrophes from the system.

At this point, we will briefly introduce each of the models or systems in this work. From this point on, assume that ecosystem, system, and species all refer to models or parts of models that are hypothetical closed models. In chapter one, we will examine two systems. First, we will look at the simple systems of exponential growth and decay. Then, we shall examine the logistic model, which places a maximum population or environmental carrying capacity on the species.

In chapters two, three, and four, we will examine systems of two species. In chapter two we shall examine the most basic model for competition between two species. A predator-prey relationship, the Lotka-Volterra model, will be examined in chapter three. Finally in chapter four, we will examine a modification of the Lotka-Volterra model allowing for the environmental carrying capacity of the prey species.

Ecosystems with three species are studied in chapters five and six. In chapter five, we examine a system of three competing species with environmental carrying capacities. In chapter six, two systems are studied. First, we examine a system of two competitors and one predator. In this model, the predator preys upon the competitors.

The final system examined in this work consists of three different levels. There is a prey species following the logistic model. This species is preyed upon by the second species. The third species of this system preys on only the second species. Thus, this third species is at the top of the three level chain of this system.

The systems we examine above are only a few of the combinations pos-



sible. There are at least eleven different systems with three species. Unfortunately, we are not able to examine them all at this time.

During the examinations of each system in this work, we seek to find the conditions for asymptotic stability. At a point of this nature, all species with nonzero populations will coexist. The purpose of this work is to find, and interpret when possible, the parameters which yield this ecological balance.

## **Chapter 1**

# **Ecosystems of One Species**

Differential equations can be used to describe hypothetical ecosystems. This paper is a study of some simple differential equations which can describe how a species functions in an ecosystem. This first chapter focuses on closed ecosystems of one hypothetical species. These systems are described by the one differential equation of the single species.

We begin the development of differential equations of population dynamics with the assumption that the growth of a species is proportional to its population. The growth rate or change in the species population can be described by the derivative of the existing number of living members of the population with respect to time. Thus, if  $N$  is the number of species present and  $t$  is time, then:

$$\frac{dN}{dt} = rN$$

While we do not know much about the the population of our species at a certain point in time (this is described by the function  $N(t)$ ), we can apply some calculus and algebra to determine more about the population. First, we can plot the derivative  $\frac{dN}{dt}$  versus  $N$  as in figure 1.1. The derivative  $\frac{dN}{dt}$  will be zero when  $N = 0$ . Thus,  $N = 0$  is a critical point where the population change is zero. A point of this nature is an equilibrium of the population.

In the graph on the derivative versus the population, assume  $r$ , the growth rate, is positive. If  $N > 0$ , then the derivative is also greater than zero. This implies that if the population is any amount more than zero then it will grow further from zero. For this reason, if  $r > 0$ ,  $N = 0$  is called an unstable equilibrium.

Now, if  $r < 0$ , then the derivative would be negative for any positive population  $N$ . This would force the population to change or grow negatively and decay toward a population of zero. If this population with negative  $r$  were perturbed some small amount from its equilibrium at zero, it would decay back to its original equilibrium, zero. This is the characterization of a stable equilibrium.

Unlike many systems of differential equations, the system  $\frac{dN}{dt} = rN$  can be solved. The solution is

$$N(t) = Ce^{rt}$$

where  $C$  is a constant.<sup>1</sup>

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<sup>1</sup>Boyce, William, and Richard DiPrima. Elementary Differential Equations and Boundary Value Problems. New York: Wiley, 1986. pg 53.

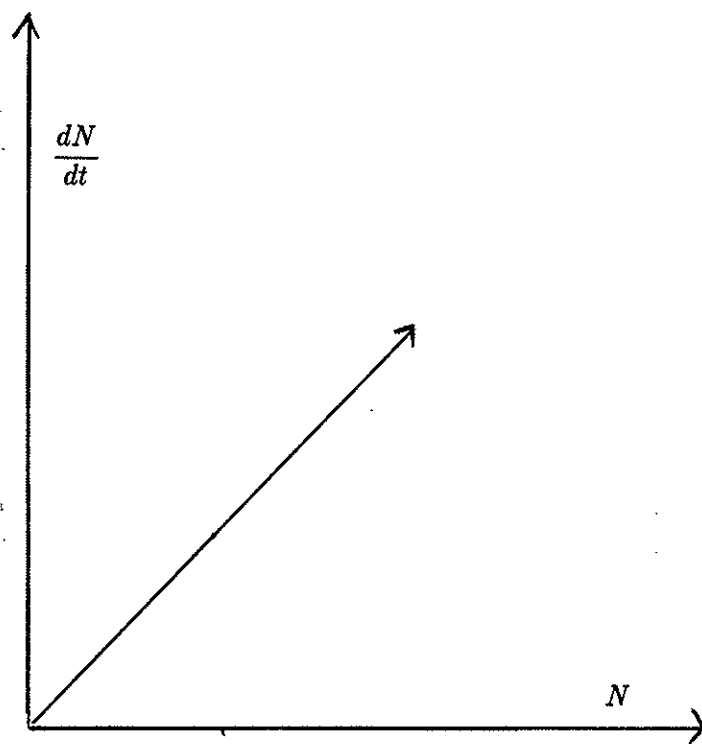


Figure 1.1: Plotting  $\frac{dN}{dt}$  versus  $N$  with  $r = 1$

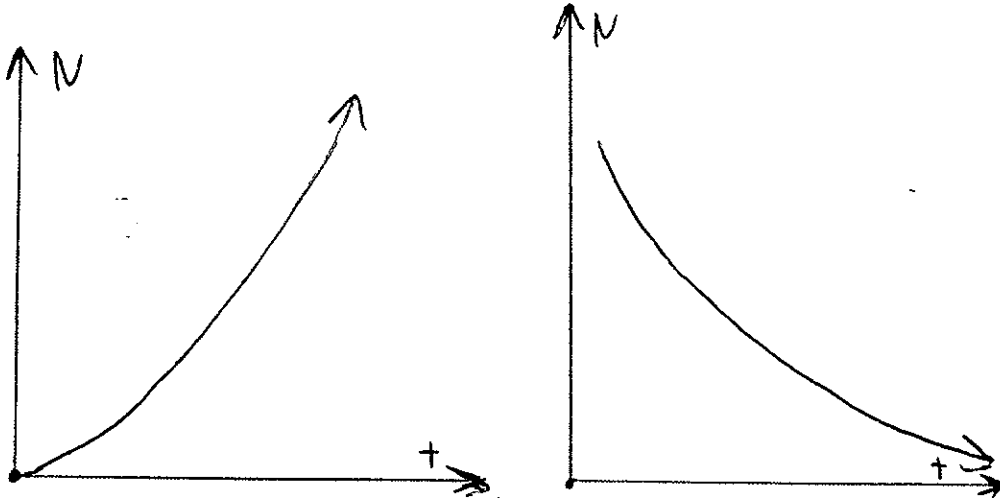


Figure 1.2: Exponential growth and decay

note  $e^{rt} > 1$ . Thus, as time increases the population is increasing. If  $r < 0$ , then  $e^{rt} < 1$  and the population decreases asymptotically to zero. The system  $\frac{dN}{dt} = rN$  is the system of exponential growth and decay applied to very simple closed environments. Examples of graphical solutions of these systems can be found in figure 1.2.

While a population may grow exponentially, or without limit, over a short period of time, it is unlikely to grow infinitely large. In an environment the population of a species is limited. Some of these limiting factors may be space in the environment, or a limited food supply for the species. These factors control the carrying capacity or upper bound of the species' population in the environment.<sup>2</sup> The logistic model is a simple model for populations which provides for the environmental carrying capacity. This basic model will be used to develop the models considered in this thesis.

The logistic model is:

$$\frac{dN}{dt} = r(1 - \frac{N}{K})N$$

---

<sup>2</sup>Boyce and DiPrima pg 55.

where  $r$  is the growth rate of the species, and  $K$  is the maximum number of members of the species the environment can support. Later, this model will be used in the simplified form  $\frac{dN}{dt} = rN - pN^2$  where  $p = \frac{r}{K}$ . Note,  $\frac{dN}{dt}$  is zero when the population is zero or  $K$ . Figure 1.3 is an example of a typical logistic model.

Assuming  $r > 0$ , one can see from the graph of  $\frac{dN}{dt}$  that the equilibria of the system occur when  $N$  is zero or  $K$ . One can also see that between zero and  $K$ , the derivative is positive. That is the population is increasing towards  $K$ . If the population is greater than  $K$ , then the derivative is negative and the population must be decreasing. Thus, zero is an unstable equilibrium and  $K$  is an asymptotically stable equilibrium. It is also worth noting that the stable equilibrium,  $K$ , of this system is independent of the growth rate  $r$  for  $r$  greater than zero..

The logistic model can be solved for the population  $N$  by separation of the variables.<sup>3</sup> The result is:

$$N(t) = \frac{K}{1 + (\frac{K}{N_0} - 1)e^{-rt}}$$

As  $t$  increases,  $e^{-rt}$  approaches zero causing  $N(t)$  to go to  $\frac{K}{1} = K$ . Thus by solving the system, we confirm the qualitative analysis.

In this section we have been able to solve the systems of differential equations under consideration. In the chapters ahead, this may be difficult if not impossible. However, the information this paper pursues about the potential for stability and coexistence between species can be obtained by purely qualitative methods.

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<sup>3</sup>Boyce and DiPrima pg 57.

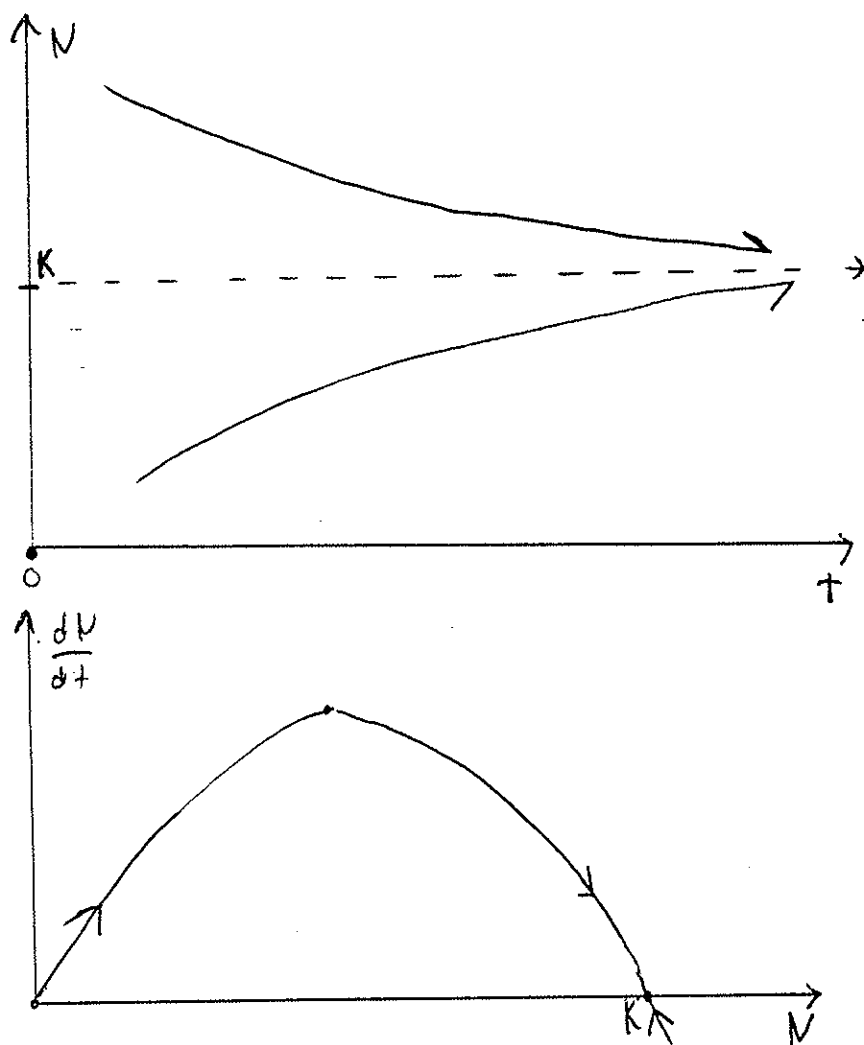


Figure 1.3: A model with logistic growth

## **Chapter 2**

# **Ecosystems of Two Species: Competition**



We begin examining the mathematical systems of hypothetical environments with systems of two species. Two species may effect each other in three different ways. First, they may compete with each other for certain resources. Second, they may mutually aid each other, a symbiotic relationship. Finally, one species may prey upon the other.

In this chapter, we will examine a model of competing species. In the next chapter, we will examine famous Lotka-Volterra model of predators and prey. A modified version of the Lotka-Volterra model will be developed and analyzed in chapter four. For now, we choose to set aside the symbiotic relationship.

The model of competing species is based on the logistic model discussed in chapter one. Let  $x$  and  $y$  be two species which share and compete for some environmental resource. The logistic model of these two species if they did not effect each other is:

$$\begin{aligned}\frac{dX}{dt} &= r_1X - p_1X^2 \\ \frac{dY}{dt} &= r_2Y - p_2Y^2\end{aligned}$$

where  $r$  is the growth rate of the species and  $p$  is the influence of the carrying capacity.

This model does not allow for interspecies competition. To allow for this we introduce the parameter  $a$ . Let  $a$  be a measure of the effect of one species on the other and  $a > 0$ . Then the system above can be modified to:

$$\begin{aligned}\frac{dX}{dt} &= r_1X - p_1X^2 - a_1XY \\ \frac{dY}{dt} &= r_2Y - p_2Y^2 - a_2XY\end{aligned}$$

In this model, we have assumed that the effect of the competition is proportional to the number of potential interactions between the two species. This potential can be related to the product of the populations,  $XY$ . The parameter  $a$ , found in each of equation of the system, described the impact of the competition on a species.

Next, let us look at a specific example of this system:

$$\begin{aligned}\frac{dX}{dt} &= 1.5X - X^2 - .5XY \\ \frac{dY}{dt} &= 2Y - Y^2 - .75XY\end{aligned}$$

Equilibria for the system will exist where the population is not changing, or where the derivatives  $\frac{dX}{dt}$  and  $\frac{dY}{dt}$  are zero. These equilibria are: (0,0), (0,2), (1.5,0), and (.8,1.4).

This system can also be looked at another way:

$$\begin{aligned}\frac{dX}{dt} &= (1.5 - X - .5Y)X \\ \frac{dY}{dt} &= (2 - Y - .75X)Y\end{aligned}$$

If  $X$  is not zero, then the derivative will be zero when  $1.5 - X - .5Y = 0$ . This is the equation for a line. The points on this line have  $\frac{dX}{dt} = 0$  so the  $X$  species population is not changing. This special line is called the  $x$ -isocline and is denoted by  $\iota_x$ . Similarly for the  $Y$  species, the points on  $2 - Y - .75X = 0$  are on the  $Y$ -isocline,  $\iota_y$ .

Next refer to figure 2.1 and note the positions of the equilibria and isoclines. Numerical analysis gives us the trajectories of this system in the figure. Note these trajectories go toward the equilibrium at (.8,1.4). Thus, computer generated approximate solutions suggest an asymptotically stable equilibrium at this point.

Before continuing it may be helpful to look at another example. Consider the system:

$$\begin{aligned}\frac{dX}{dt} &= (1.5 - X - .5Y)X \\ \frac{dY}{dt} &= (2 - .5Y - 1.5X)Y\end{aligned}$$

By setting the derivatives to zero we find the equilibria at (0,0), (0,4), (1.5,0), and (1,1).

From figure 2.2, a computer approximation of several trajectories of the system we can see that this system appears to have an unstable equilibrium at the point (1,1). Also, note the relationship between the isoclines.

While these two systems of competitors started from the same model, they give quite different results. In one the species coexist and in the other they do not. This difference must result from the parameters  $r$ ,  $p$ , and  $a$ , which are different in each of the systems.

Now we return to the equations of the isoclines. The general equations of  $\iota_x$  and  $\iota_y$  are:

$$\begin{aligned}r_1 - p_1X - a_1Y &= 0 \\ r_2 - p_2Y - a_2X &= 0\end{aligned}$$

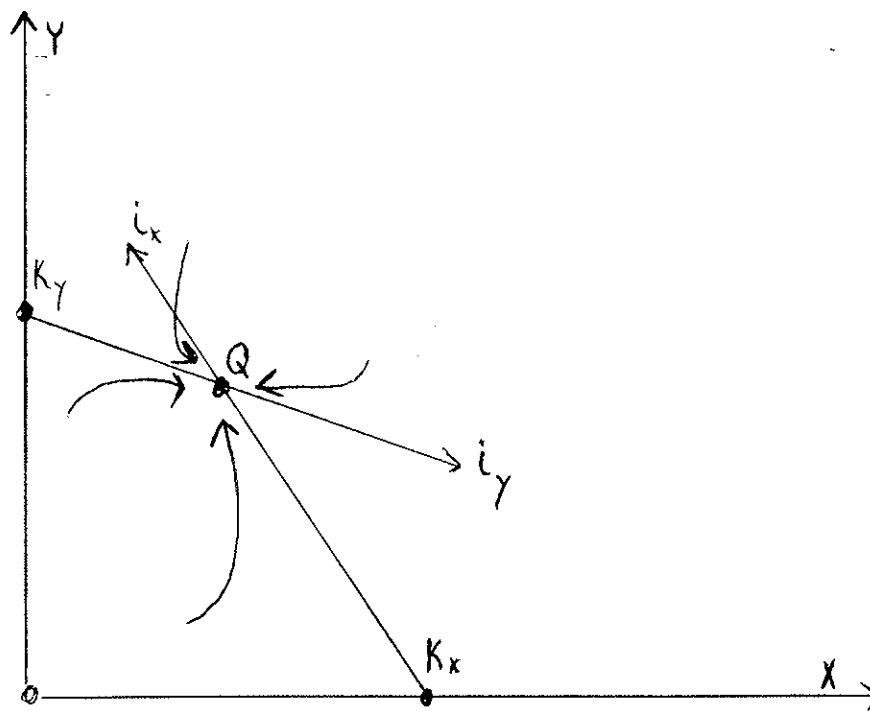


Figure 2.1: Two coexisting competitors.

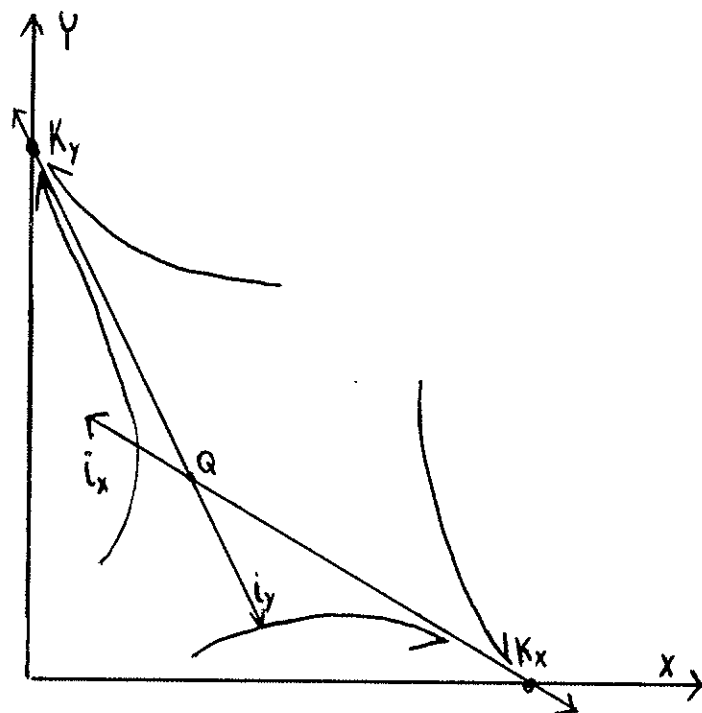


Figure 2.2: Two non-coexisting competitors.

From these equations we can find the x and y intercepts of the isoclines. The x-intercept of  $\iota_x$  is  $\frac{r_1}{p_1}$  and its y-intercept is  $\frac{r_1}{a_1}$ . Similarly, the x-intercept of  $\iota_y$  is  $\frac{r_2}{a_2}$  and its y-intercept is  $\frac{r_2}{p_2}$ .

In the example of the two competing species with coexistence the y-intercept of  $\iota_x$  is greater than the y-intercept of  $\iota_y$ . This is contrary to the situation in the example without coexistence. Thus, we hypothesize that one condition for the coexistence of competitors is  $\frac{r_1}{a_1} > \frac{r_2}{p_2}$ . Similarly, from observing the x-intercept of  $\iota_y$  is greater than that of  $\iota_x$ , we hypothesize another condition for coexistence is  $\frac{r_2}{a_2} > \frac{r_1}{p_1}$ .

If  $\frac{r_1}{a_1} > \frac{r_2}{p_2}$ , then  $\frac{p_2}{a_1} > \frac{r_2}{r_1}$ . Similarly from the second inequality above, we obtain  $\frac{r_2}{r_1} > \frac{a_2}{p_1}$ . These inequalities can be combined to give the inequality:

$$\frac{p_2}{a_1} > \frac{r_2}{r_1} > \frac{a_2}{p_1} \quad (2.1)$$

Before attempting to prove the above inequality is required for coexistence of the two species, we first must be sure there really exists an equilibrium in the first quadrant. If there is no equilibrium in the first quadrant there can be no asymptotically stable equilibrium or point of coexistence for the species. We must find conditions which give the conjecture a chance.

The equilibrium we must have in the first quadrant is the intersection of the isoclines. By solving one isocline for  $y$  and substituting it into the other we obtain the equilibrium

$$\left( \frac{-r_1 p_2 + a_1 r_2}{-p_2 p_1 + a_2 a_1}, \frac{-r_2 p_1 + a_2 r_1}{-p_2 p_1 + a_2 a_1} \right)$$

We must have this equilibrium in the first quadrant. First, note the denominators are the same for the x and y coordinate. If condition 2.1 holds, then this denominator must be negative for  $a_1 a_2 < p_1 p_2$ . Similarly condition 2.1 forces both numerators to be negative. Thus, both fractions in the equilibrium point are positive if our conjecture is true, and the equilibrium must be in the first quadrant. For reference purposes let this equilibrium be called  $Q$ .

So far we have two isoclines intersecting in certain way in the first quadrant. In figure 2.3, note that the isoclines divide the first quadrant into four parts or subquadrants:  $\Gamma_1$ ,  $\Gamma_2$ ,  $\Gamma_3$ , and  $\Gamma_4$ .

If a point in the first quadrant is to the left or below  $\iota_x$  then  $r_1 - p_1 X - a_1 Y > 0$ , and  $\frac{dX}{dt} > 0$ . Similarly if a point is to the right or above  $\iota_x$ ,  $\frac{dX}{dt} < 0$ . This same pattern holds for  $\iota_y$ . If a point is to the left or below

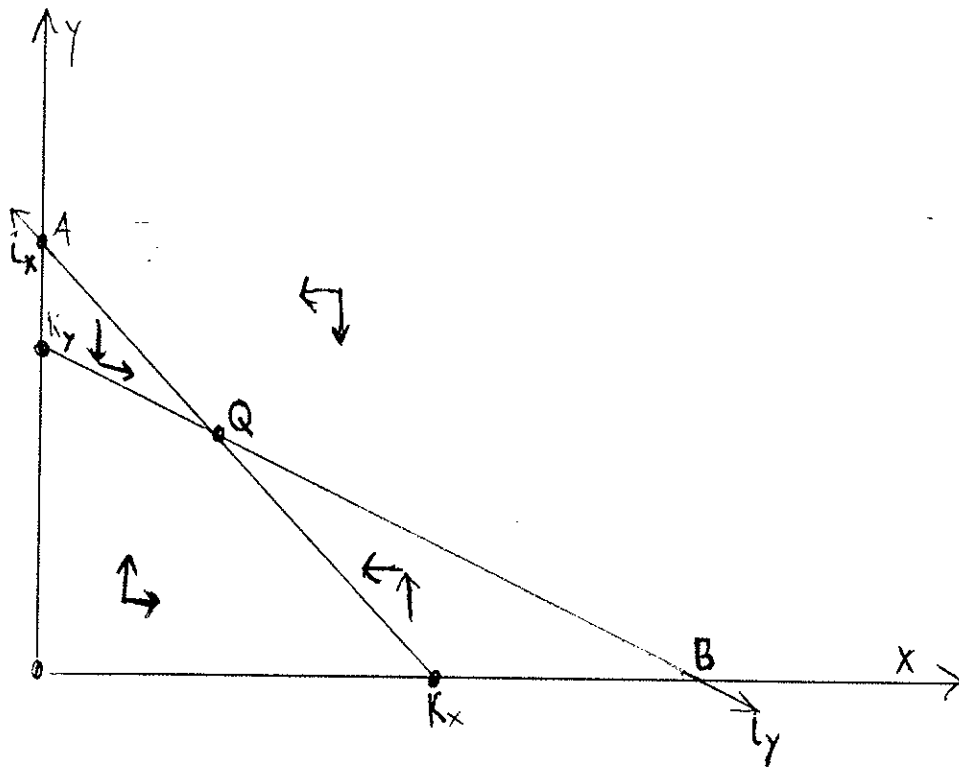


Figure 2.3: Isoclines dividing the first quadrant.

| <i>subquadrant</i> | <i>Y-species</i> | <i>X-species</i> |
|--------------------|------------------|------------------|
| $\Gamma_1$         | decreasing       | decreasing       |
| $\Gamma_2$         | decreasing       | increasing       |
| $\Gamma_3$         | increasing       | increasing       |
| $\Gamma_4$         | increasing       | decreasing       |

Table 2.1: Population change in the first quadrant.

this isocline, then  $\frac{dY}{dt} > 0$ . If a point is to the right or above  $\iota_y$ ,  $\frac{dY}{dt} < 0$ . Recalling that a positive derivative describes an increasing population and a negative derivative describes a decreasing population, we can construct table 2.1 based on figure 2.3.

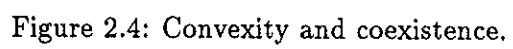
From table 2.1, we construct the arrows in figure 2.3 describing the trajectories of the solutions to the competitive system meeting condition 2.1. In every subquadrant the trajectories must move toward  $Q$ . Thus, for the condition 2.1 the competitive system described in this chapter is asymptotically stable and  $Q$  is the point of coexistence of the two species.

An interesting biological note follows from the above proof. Recall the statement  $a_1a_2 < p_1p_2$ . If we can assume there is an equilibrium in the first quadrant and only this abbreviated condition is true, then we can work backwards to the condition 2.1. This abbreviated condition implies the impact of competition must be relatively small when compared to the impact of other environmental conditions for species to coexist. This condition is not surprising. Two species that are mildly competitive will coexist and two species which compete too aggressively cannot.

As a final note, refer to the figure 2.4. Note the area bounded by the x-axis, y-axis, and segments of the isoclines from the environmental carrying capacities  $K_x$  and  $K_y$  to  $Q$ . This area,  $\Gamma_3$  is convex<sup>1</sup>. Let  $A$  be the y-intercept of  $\iota_x$  and  $B$  the x-intercept of  $\iota_y$ .  $\Gamma_3$  is the finite intersection of convex sets. In particular, the intersection of triangles:  $\triangle AK_xO$  and  $\triangle K_yBO$  form  $\Gamma_3$ . From figure 2.4, one can see that condition 2.1 is equivalent with the convexity of  $\Gamma$ . We will return to the subject of convexity and coexistence in a later chapter.

---

<sup>1</sup>A set  $S$  is convex if the line segment between any two points in  $S$  contains only points in  $S$ .





## Chapter 3

# The Lotka-Volterra Model

In this chapter, we will look at the Lotka-Volterra system of two species in a closed environment. This hypothetical system assumes the only interaction in the environment occurs between the predator and prey species. We begin by developing the model. Then, we will qualitatively analyze its characteristics and make some biological interpretations.

The Lotka-Volterra model begins with several assumptions about the populations of the species.

1. If there are no predators, the prey's growth is proportional to its population. Thus, if  $X$  is the prey species,  $\frac{dX}{dt} = r_1X$ ,  $r_1 > 0$ , in the absence of the predator.
2. Without the presence of prey, the predator  $Y$  dies out. So,  $\frac{dY}{dt} = -r_2Y$ ,  $r_2 > 0$  if no prey are present.
3. The number of interactions between predator and prey is proportional to the product of the predator and prey populations. The predator's growth rate will be increased by interactions with the prey,  $a_2XY$ ,  $a_2 > 0$ . At the same time, the prey's growth rate will be reduced by the interactions,  $-a_1XY$ <sup>1</sup>.

As a result of these assumptions, we can develop the Lotka-Volterra system:

$$\begin{aligned}\frac{dX}{dt} &= r_1X - a_1XY = (r_1 - a_1Y)X \\ \frac{dY}{dt} &= -r_2Y + a_2XY = (-r_2 + a_2X)Y\end{aligned}\tag{3.1}$$

Before we attempt to analyze this system, we look at a typical example of a Lotka-Volterra system.

$$\begin{aligned}\frac{dX}{dt} &= 2X - XY \\ \frac{dY}{dt} &= -Y + 1.5XY\end{aligned}$$

Figure 3.1 gives several of the solutions to this example. This figure suggests that the solutions of the system will be elliptical paths about some center. If this is true, then this center is stable equilibrium<sup>2</sup>. A stable equilibrium

<sup>1</sup>Boyce and DiPrima. pg 473 gives a more detailed description.

<sup>2</sup>A critical point is stable if trajectories that start relatively close to the equilibrium stay relatively close to the equilibrium. A more concise definition can be found in Boyce and DiPrima. pg 442.

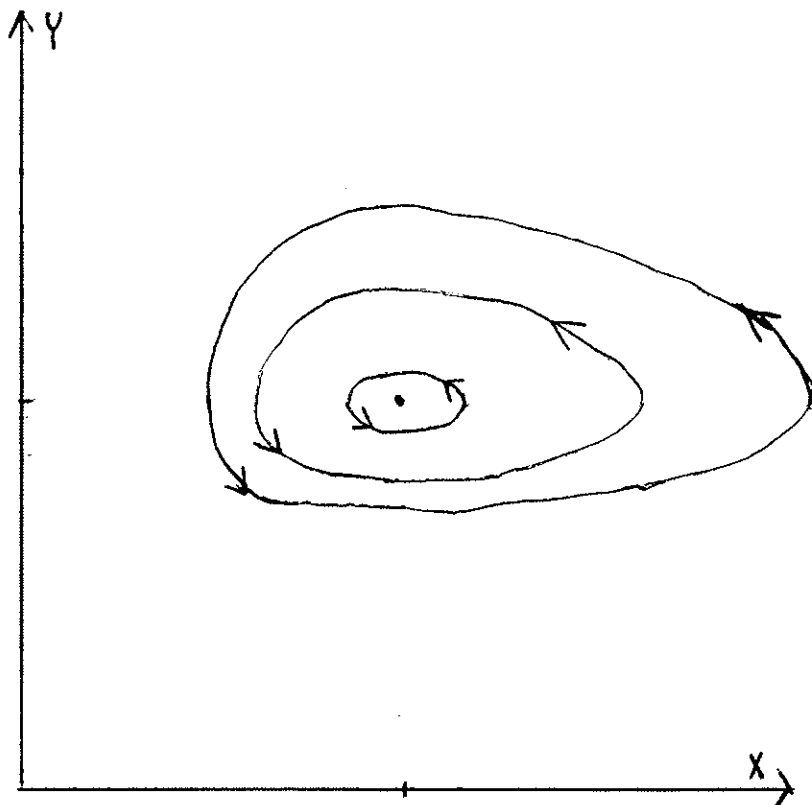


Figure 3.1: Several solutions to a Lotka-Volterra system.

is characterized by solutions neither moving toward or away from the equilibrium. In this case, the solutions appear to revolve about the equilibrium.

The first step in the analysis of this system is to determine the location of the equilibria. By setting  $\frac{dX}{dt}$  and  $\frac{dY}{dt}$  equal to zero we can find the equilibria of system 3.1. These are  $(0, 0)$  and  $(\frac{r_2}{a_2}, \frac{r_1}{a_1})$ . Also of importance are the isoclines. Borrowing the notation of the previous chapter, we have  $\iota_x$  as the line  $Y = \frac{r_1}{a_1}$ . Similarly,  $\iota_y$  is the line  $X = \frac{r_2}{a_2}$ .

Note, if  $X < \frac{r_2}{a_2}$  or left of  $\iota_y$ , then  $\frac{dY}{dt} < 0$ . If  $X > \frac{r_2}{a_2}$  or to the right, then  $\frac{dY}{dt} > 0$ . Also, if  $Y < \frac{r_1}{a_1}$ , below  $\iota_x$ ,  $\frac{dX}{dt} > 0$ , and if  $Y > \frac{r_1}{a_1}$ , above, then  $\frac{dX}{dt} < 0$ .

The isoclines<sup>3</sup> of the general Lotka-Volterra system are graphed in fig-

<sup>3</sup>Isoclines are lines in the phase plane where one species rate of growth is constant. In this paper, isocline will refer to a line in the phase plane where the rate of growth is zero. The isoclines are given by the linear factor of the factored mathematical system.

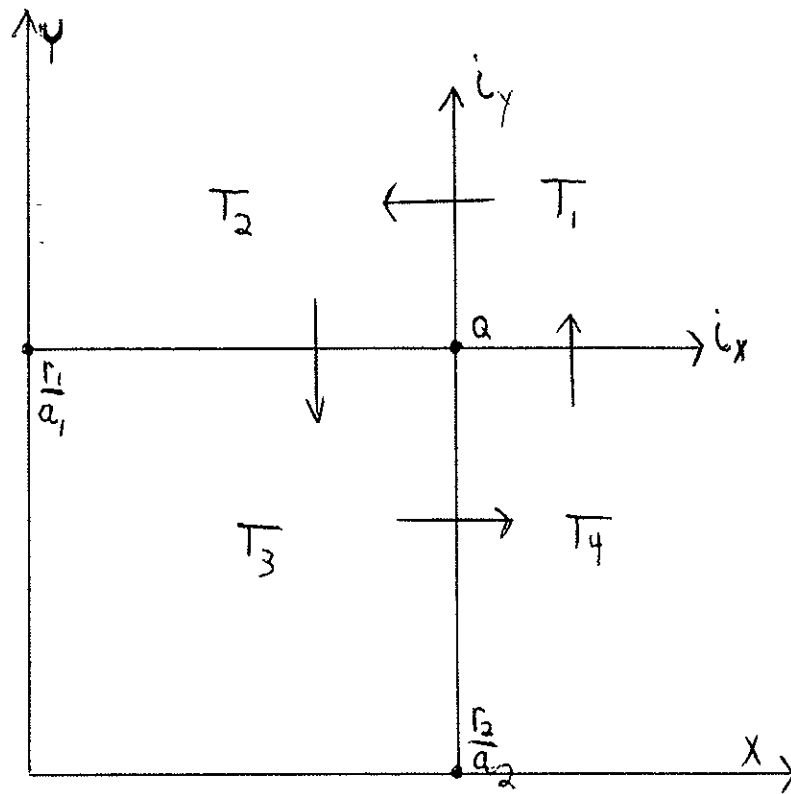


Figure 3.2: Isoclines and growth in general

| <i>Quadrant</i> | <i>X population</i> | <i>Y population</i> |
|-----------------|---------------------|---------------------|
| $\Gamma_1$      | decreasing          | increasing          |
| $\Gamma_2$      | decreasing          | decreasing          |
| $\Gamma_3$      | increasing          | decreasing          |
| $\Gamma_4$      | increasing          | increasing          |

Table 3.1: Population change in the subquadrants of the Lotka-Volterra system.

ure 3.2: The equilibrium at the intersection of the isoclines is  $Q$ . The subquadrants of the first quadrant formed by the isoclines are labelled with  $\Gamma$  as in the previous chapter. The arrows in the figure are constructed from the information from the paragraph above summarized in table 3.1.

From the evidence so far, it would seem that indeed the solutions or trajectories of system 3.1 are elliptical or circular. To prove this, choose a point near the equilibrium  $Q$ , say  $(\frac{r_2}{a_2} + u, \frac{r_1}{a_1} + v)$ . From this we can obtain:

$$\begin{aligned}\frac{du}{dt} &= \frac{-a_1 r_2 v}{a_2} - a_1 u v \\ \frac{dv}{dt} &= \frac{r_1 a_2 u}{a_1} + a_2 u v\end{aligned}$$

Because we have chosen  $u$  and  $v$  to be small, we can ignore the nonlinear terms and reduce this system to:

$$\begin{aligned}\frac{du}{dt} &= \frac{-a_1 r_2 v}{a_2} \\ \frac{dv}{dt} &= \frac{r_1 a_2 u}{a_1}\end{aligned}$$

Now near  $Q$  we have

$$\frac{du}{dv} = \frac{\frac{du}{dt}}{\frac{dv}{dt}} = \frac{\frac{-a_1 r_2 v}{a_2}}{\frac{r_1 a_2 u}{a_1}}$$

By separating the variables this expression can be integrated to give

$$\frac{r_1 a_2}{a_1} u^2 + \frac{a_1 r_2}{a_2} v^2 = k$$

The constants of integration combine to give the constant  $k^4$ . The above expression is the formula for an ellipse. Thus, the solutions near the equilibrium are closed curves similar to ellipses.

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<sup>4</sup>Boyce and DiPrima. pg 478.

Earlier we hypothesized that the equilibrium of system 3.1 was stable. An equilibrium is stable if and only if the eigenvalues of the corresponding linear system near that equilibrium are purely imaginary<sup>5</sup>. The corresponding linear system of system 3.1 near  $Q = (q_1, q_2)$  is:

$$\begin{bmatrix} 0 & \frac{a_1 r_2}{a_2} \\ \frac{a_2 r_1}{a_1} & 0 \end{bmatrix} \begin{bmatrix} q_1 \\ q_2 \end{bmatrix} = 0$$

The eigenvalues of this system are the complex values of  $\lambda$  such that:

$$\begin{vmatrix} -\lambda & \frac{a_1 r_2}{a_2} \\ \frac{a_2 r_1}{a_1} & -\lambda \end{vmatrix} = \lambda^2 + r_1 r_2 = 0$$

Clearly one can see  $\lambda = \pm i\sqrt{r_1 r_2}$ . Thus, the eigenvalues of system 3.1 are purely imaginary and the system has  $Q$  as a stable equilibrium.

We now know that solutions to the Lotka-Volterra system rotate in nearly elliptical patterns about the stable equilibrium  $Q$ . It has been proven that these cycles about the equilibrium are closed<sup>6</sup>, but this is not in the focus of this project.

The solutions of the linear system above can be written as:

$$\begin{aligned} X &= \frac{r_2}{a_2} + \frac{r_2}{a_2} C \cos(\sqrt{r_1 r_2} t + \phi) \\ Y &= \frac{r_1}{a_1} + \frac{r_1}{a_1} C \sin(\sqrt{r_1 r_2} t + \phi) \end{aligned}$$

where  $C$  and  $\phi$  are determined by initial conditions<sup>7</sup>. Again, it must be clarified that these solutions are applicable only near the equilibrium.

However, we can still gather some very useful information from these solutions. First, the period of the cycle of the system is  $\frac{2\pi}{\sqrt{r_1 r_2}}$ . Thus, the time it takes for a complete cycle to occur is based only on the growth rates of the two populations. Also, by the nature of the sine and cosine functions, we see that the population of the predator is one quarter cycle behind the population of the prey. Finally, the actual populations of the species result from both the initial conditions and the parameters of the system.

The results above generally make sense. However, there is one result from the Lotka-Volterra model that causes this system to be a good model

<sup>5</sup>Boyce and DiPrima. pg 451.

<sup>6</sup>Braun, Martin. Differential Equations and their applications. New York: Springer-Verlag, 1983. pg 443.

<sup>7</sup>Boyce and DiPrima. pg 478.

for certain real ecosystems. Let us assume that something entered the environment that killed both the predator and the prey alike, for example, a pesticide applied to a population of insects. Let  $p$  denote the impact of the change in the environment and assume  $p$  is greater than zero. System 3.1 now becomes:

$$\begin{aligned}\frac{dX}{dt} &= r_1X - a_1XY - pX = (r_1 - p)X - a_1XY \\ \frac{dY}{dt} &= -r_2Y + a_2XY - pY = (-r_2 - p)Y + a_2XY\end{aligned}$$

The familiar Lotka-Volterra model has its stable equilibrium at  $(\frac{r_2}{a_2}, \frac{r_1}{a_1})$ . The modified system (pesticide) gives us the stable equilibrium at

$$\left(\frac{r_2 + p}{a_2}, \frac{r_1 - p}{a_1}\right)$$

The impact of  $p$  increases the number of prey (insects) and decreases the number of predators at the equilibrium.

Because the equilibrium is an average of the population<sup>8</sup>, it appears that this new element in the environment  $p$ , has increased the average number of prey species. In our example, this means that applying pesticide increased the population of a species that it killed. This occurrence is known as the Volterra principle.

The Volterra principle is an effect of the Lotka-Volterra model. Some populations follow this unique pattern. These populations are well modeled by the Lotka-Volterra model. For other systems without this pattern, other models for a predator and prey population are needed. In the next chapter, we consider another system describing an ecosystem with only two species in it, one predator and one prey.

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<sup>8</sup>It can be proven that this equilibrium is the average. A proof can be found in Braun pg 445.

## Chapter 4

# The Modified Lotka-Volterra Model



In the last chapter we examined the Lotka-Volterra model of two species in a predator-prey relationship. Also, we observed the Volterra principle. In an attempt to improve on this apparent contradiction, this chapter considers a modification of the Lotka-Volterra system. First, note that the Lotka-Volterra model does not allow for an environmental carrying capacity for the prey. In fact, the model assumes in the absence of the predator, the prey grows without bound. This is where we can make a modification.

Let  $p$  be the logistic parameter limiting the maximum population of the prey species  $X$ . Then the Lotka-Volterra model can be changed to<sup>1</sup>:

$$\begin{aligned}\frac{dX}{dt} &= (r_1 - a_1Y - pX)X \\ \frac{dY}{dt} &= (-r_2 + a_2X)Y\end{aligned}\tag{4.1}$$

As with the other models we have examined, let us look at the equilibria of this system first. Setting  $\frac{dX}{dt}$  and  $\frac{dY}{dt}$  equal to zero, we find the equilibria at:  $(0, 0)$ ,  $(\frac{r_1}{p}, 0)$ , and  $Q$ , where  $Q$  is the intersection of the isoclines. The  $Y$ -isocline,  $\iota_y$ , is still the line  $X = \frac{r_2}{a_2}$ . The  $X$ -isocline,  $\iota_x$  is  $Y = \frac{r_1}{a_1} - \frac{p}{a_1}X$ . The equilibrium we must have in the first quadrant is  $Q$ , or specifically:

$$\left( \frac{r_2}{a_2}, \frac{p(\frac{r_1}{p} - \frac{r_2}{a_2})}{a_1} \right)\tag{4.2}$$

Let  $A = \frac{r_1}{p} - \frac{r_2}{a_2}$ . If  $A$  is greater than zero,  $Q$  will be in the first quadrant. As a conjecture we give: If  $A > 0$ , then  $Q$  will be an asymptotically stable equilibrium in the first quadrant. Now, let  $Q$  be written as  $(\frac{r_2}{a_2}, \frac{pA}{a_1})$ .

To examine the nature of system 4.1, we look at the corresponding linear systems near each of the equilibria. In particular, we seek the eigenvalues of the system at these points. For an equilibrium  $(x, y)$ , the eigenvalues are obtained from:

$$\begin{vmatrix} r_1 - a_1Y - 2pX - \lambda & -a_1X \\ a_2Y & -r_2 + a_2X - \lambda \end{vmatrix} = 0$$

First, examine the system at  $(0, 0)$ . The eigenvalues will be the values of  $\lambda$  such that:

$$\begin{vmatrix} r_1 - \lambda & 0 \\ 0 & -r_2 - \lambda \end{vmatrix} = (r_1 - \lambda)(-r_2 - \lambda) = 0$$

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<sup>1</sup>This modification is suggested in Boyce and DiPrima pg 479.

Thus,  $\lambda = r_1$  or  $\lambda = -r_2$ . Because the eigenvalues of this system are both real, one is positive, and one is negative, we know how solutions of system 4.1 behave near this equilibrium. The equilibrium  $(0, 0)$  is an unstable saddle. This means solutions approach the equilibrium along one eigenvector and then move away from the equilibrium along the other eigenvector<sup>2</sup>.

Next, we turn to the equilibrium at  $(\frac{r_1}{p}, 0)$ . The eigenvalues at this equilibria are determined by:

$$\begin{vmatrix} -r_1 - \lambda & -\frac{a_1 r_1}{p} \\ 0 & -r_2 + \frac{a_2 r_1}{p} - \lambda \end{vmatrix} = (-r_1 - \lambda)(-r_2 + \frac{a_2 r_1}{p} - \lambda) = 0$$

Solving the first factor gives us the negative eigenvalue  $\lambda = -r_1$ . The second eigenvalue is found at  $\lambda = -r_2 + \frac{a_2 r_1}{p}$ . Because  $A$  is greater than zero by our assumption, we have  $\frac{r_1}{p} > \frac{r_2}{a_2}$ . Thus the second eigenvalue will be positive. Here again, there are two real eigenvalues of opposite sign. This equilibrium is also an unstable saddle.

So far,  $Q$  is the only equilibrium candidate remaining that could be the asymptotically stable equilibrium of the system. In fact, we have found the other two equilibria both to be unstable saddle points. Now, we proceed to work with  $Q$ . The eigenvalues for  $Q$  are determined by:

$$\begin{vmatrix} r_1 - pA - 2\frac{pr_2}{a_2} - \lambda & -\frac{a_1 r_2}{a_2} \\ \frac{a_2 pA}{a_1} & -\lambda \end{vmatrix} = \lambda^2 + (pA - r_1 + 2\frac{pr_2}{a_2})\lambda + pr_2 A = 0$$

This is a quadratic equation in  $\lambda$ . Note the coefficient of  $\lambda$  simplifies to  $\frac{pr_2}{a_2}$ . Applying the quadratic formula gives:

$$\lambda = \frac{-\frac{pr_2}{a_2} \pm \sqrt{(\frac{pr_2}{a_2})^2 - 4pr_2 A}}{2}$$

If the discriminant is positive, it is smaller than  $(\frac{pr_2}{a_2})^2$ . This relation forces the square root to be smaller than the first term in the numerator of the values for  $\lambda$ . Thus, we will have two unequal, negative, and real eigenvalues. This condition is equivalent to an asymptotically stable improper node<sup>3</sup> at  $Q$ . All trajectories of this system must approach the equilibrium along the eigenvectors.

<sup>2</sup>For a more concise definition of the unstable saddle, see Boyce and DiPrima pg. 429.

<sup>3</sup>This is explained in Boyce and DiPrima. pg 428

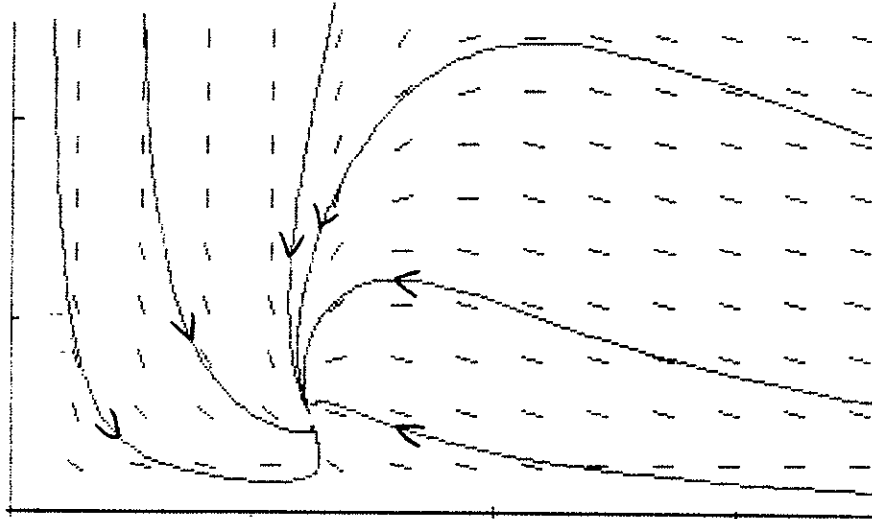


Figure 4.1: A typical system with  $Q$  as an improper node.

If the discriminant is negative, the values of  $\lambda$  will be complex. The real part of the two different complex eigenvalues will be negative. This is equivalent to having  $Q$  as an asymptotically stable spiral equilibrium<sup>4</sup>.

If the discriminant were equal to zero, we would then have two equal, real, negative eigenvalues. This condition is equivalent to the asymptotically stable proper node<sup>5</sup>.

Figure 4.1 is an example of a system with an improper node. An example of a system with a spiral point is given in figure 4.2. Figure 4.3 is an example giving the trajectories a system if the equilibrium  $Q$  is a proper node. Each system in these examples follows the form of the general system 4.1.

Each of the three types of equilibria generated at  $Q$  by this system is asymptotically stable for  $A > 0$ . Because  $Q$  is of this nature, all trajectories will tend to  $Q$ . This implies all populations will tend to this equilibrium. The species of this system tend to coexist as they did in the Lotka-Volterra model. However, in this modified system 4.1, each species tends toward some population.

In the Lotka-Volterra model, if the system is disturbed from its stable

<sup>4</sup>This is explained in Boyce and DiPrima. pg 433.

<sup>5</sup>This is explained in Boyce and DiPrima. pg 430.

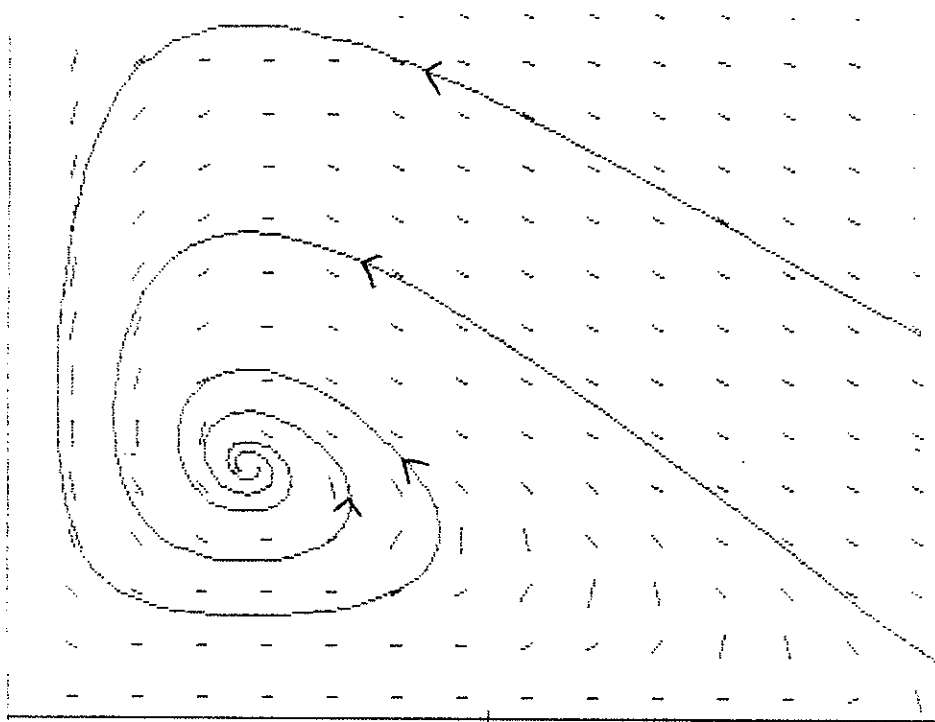


Figure 4.2: A typical system with  $Q$  as a spiral point.

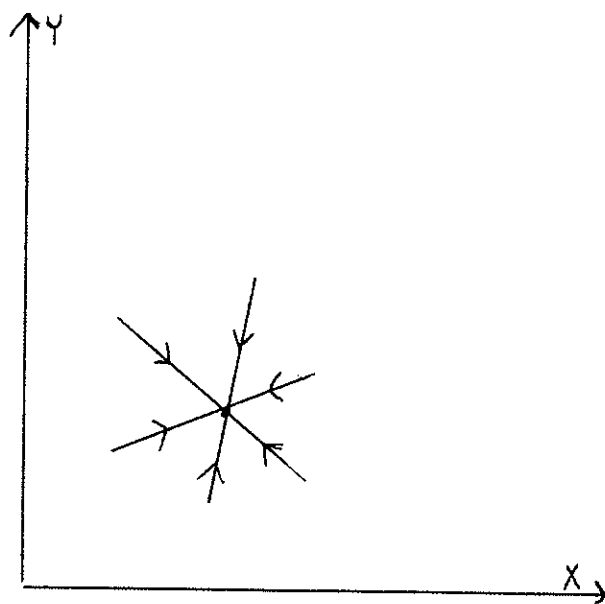


Figure 4.3: A typical system with  $Q$  as a proper node.

equilibrium it follows a cycle until disturbed again. This result is another difference between the Lotka-Volterra model and real ecosystems. In real ecosystems, when species are disturbed from their equilibrium, they tend to return to that equilibrium over time. This does not happen in the Lotka-Volterra model.

In the modified Lotka-Volterra model, system 4.1, the disturbed species tends to return to its equilibria over time. Thus, this hypothetical mathematical system more accurately follows real ecosystems.

Now, recall the Volterra principle. This principle is one reason some find the Lotka-Volterra system invalid. Applying the parameter  $i$  to the system 4.1 gives us the system<sup>6</sup>

$$\begin{aligned}\frac{dX}{dt} &= r_1X - a_1XY - pX^2 - iX = ((r_1 - i) - a_1Y - pX)X \\ \frac{dY}{dt} &= -r_2Y + a_2XY - iY = ((-r_2 - i) + a_2X)Y\end{aligned}\quad (4.3)$$

This system with the parameter  $i$  is just another system like system 4.1. The equilibrium of system 4.1 can be written

$$\left( \frac{r_2}{a_2}, \frac{r_1 - \frac{pr_2}{a_2}}{a_1} \right)$$

After the parameter  $i$  enters the system, the equilibrium becomes

$$\left( \frac{r_2 + i}{a_2}, \frac{r_1 - \frac{pr_2}{a_2} - (i + \frac{ip}{a_2})}{a_1} \right)$$

Adding the parameter  $i$ , which harmed both species, to the system caused the average population of the predator to drop. Also, it increased the population of the prey. This is the Volterra principle. This principle also occurs in our modification of the Lotka-Volterra system. Thus, system 4.1 can also be a model for systems with this property.

As a modification of system 4.3, consider a different parameter  $i$ . Let this new  $i$  be an inhibiting factor on the prey species only. That is, let the  $i$  in the  $Y$  derivative of system 4.3 be zero. The above equilibrium of the modified system 4.3 now becomes

$$\left( \frac{r_2}{a_2}, \frac{r_1 - \frac{pr_2}{a_2} - i}{a_1} \right)$$

---

<sup>6</sup>A good way to think about  $i$  is to imagine an insecticide killing both predator and prey insects.

Notice that the average population of the prey, the  $x$ -coordinate of the equilibrium, is the same as it was before the parameter  $i$  was introduced. However, the average population of the predator, which is unharmed by  $i$  drops as a result of the impact of  $i$  on the prey! Thus, according to this hypothetical model<sup>7</sup>, applying insecticides will not decrease the population of the species it is applied to kill, but it will reduce the numbers of the predators of the prey species<sup>8</sup>.

While the system 4.1 behaves somewhat differently than the Lotka-Volterra model, the Volterra principle and its modification still remain. It is also worth noting that the parameter  $a_1$  plays no role in determining the eigenvalues at the equilibria. This implies that  $a_1$ , the impact of predation on the prey, does not have any influence on the nature of the equilibrium  $Q$ . In simple words, the impact of the predator on the prey does not effect the tendency of the species of system 4.1 to coexist.

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<sup>7</sup>The same result occurs in the Lotka-Volterra model.

<sup>8</sup>The effect of DDT on predators is an example of this.

## **Chapter 5**

# **A Model for Three Species: Competition**

### **5.1 The Model and Equilibria**

In the previous chapters we have examined several mathematical systems with one or two variables. In these systems, each variable represented the population of one species. Now, we move into the study of closed hypothetical ecosystems containing three species. In these systems, there will exist three variables:  $X$ ,  $Y$ , and  $Z$ . The transition from two variables to three is not as easy as changing from one variable to two. With three variables, graphs are more complicated. Also, the eigenvalues of a system are much more difficult to find. As a result of these complications, the work in this chapter is not complete.

The goal of this chapter is to examine the closed hypothetical ecosystem of three competing species. In particular, we seek to find the conditions equivalent to the coexistence of all three species. The system studied in this chapter is an extension of the system developed in chapter two. This system is based on several assumptions:

1. In the absence of the other two species, each species will follow the logistic model of growth. That is, each species will have a positive growth rate  $r$  and an environmental limitation  $p$ , where  $p$  is positive.
2. Each species will be inhibited by each of the other species by some positive parameter  $a$ ,  $b$ , or  $c$ .
3. The only interaction between the species is competition for resources. No species preys upon either of the other two.

The system under consideration in this chapter is

$$\begin{aligned}\frac{dX}{dt} &= r_1X - b_1XY - c_1XZ - p_1X^2 \\ \frac{dY}{dt} &= r_2Y - a_2XY - c_2YZ - p_2Y^2 \\ \frac{dZ}{dt} &= r_3Z - a_3XZ - b_3YZ - p_3Z^2\end{aligned}$$

The first step to evaluating this system is to find the equilibria of this system. To simplify the task, factor the above system to get

$$\begin{aligned}\frac{dX}{dt} &= (r_1 - b_1Y - c_1Z - p_1X)X \\ \frac{dY}{dt} &= (r_2 - a_2X - c_2Z - p_2Y)Y \\ \frac{dZ}{dt} &= (r_3 - a_3X - b_3Y - p_3Z)Z\end{aligned}\tag{5.1}$$



The equilibria of the system will exist at the points in three space where the derivatives of the system are all equal to zero. Clearly one equilibrium will be  $(0, 0, 0)$ . Next, by setting any two of the species' populations to zero, we can find the three equilibria:  $(0, 0, \frac{r_3}{p_3})$ ,  $(0, \frac{r_2}{p_2}, 0)$ , and  $(\frac{r_1}{p_1}, 0, 0)$ . These equilibria correspond to the maximum populations obtained by each species in the absence of the other two as predicted by the logistic model.

If only one of the three species has a population of zero, then the system 5.2 reduces to the system of two competing species from chapter two. The equilibria given by each of these cases are:  $(0, \frac{-p_3 r_2 + c_2 r_3}{-p_3 p_2 + c_2 b_3}, \frac{b_3 r_2 - p_2 r_3}{-p_3 p_2 + c_2 b_3})$ ,  $(\frac{b_1 r_2 - p_2 r_1}{-p_1 p_2 + b_1 a_2}, \frac{-p_1 r_2 + a_2 r_1}{-p_1 p_2 + a_2 b_1}, 0)$ , and  $(\frac{c_1 r_3 - p_3 r_1}{-p_1 p_3 + c_1 a_3}, 0, \frac{a_3 r_1 - p_1 r_3}{-p_1 p_3 + a_3 c_1})$ .

Already, it is becoming difficult to find the equilibria. The final eighth equilibrium of this system, the one in which we are most interested, is too complicated and confusing to write here. Its precise description gives us little information. For the purpose of reference, we will denote this equilibrium as the equilibrium  $E$ .

At this time, it is appropriate to introduce the idea of an isoplane. Recall from earlier chapters that the isocline of a species was the line in the plane where the derivative of a species was zero. The analog of the isocline in threespace is the isoplane. The isoplane of a species is the plane existing in threespace where the derivative of that species is zero. Like the isocline, the isoplane of a species is given by setting the complicated factor of that species' derivative in system 5.2 equal to zero. The isoplane of the species  $X$ , denoted by  $\Pi_x$  is the plane  $r_1 - b_1 Y - c_1 Z - p_1 X = 0$ . Similarly, the isoplane of species  $Y$ ,  $\Pi_y$ , is  $r_2 - a_2 X - c_2 Z - p_2 Y = 0$ , and  $\Pi_z$  is  $r_3 - a_3 X - b_3 Y - p_3 Z = 0$ .

At this point, let us return to the equilibrium  $E$ . The intersection of all three isoplanes will give another equilibrium. This equilibrium is  $E$ . While it is not correct to assume this intersection is a single point (it could be a line or a plane as well), an assumption we will make later in this paper will force this intersection to be the single point,  $E$ .

Earlier, some of the difficulties of working in the ecospace of three species were described. While some of the mathematics can get complicated, much can be learned about this system by applying eigenvalue analysis at each equilibria of the system. A fair amount of this information can be gathered by applying an eigenvalue analysis to the simpler equilibria. The eigenvalues of system 5.2 near an equilibrium  $(u, v, w)$  are given by subtracting  $\lambda$  from the diagonal elements of the following matrix and setting its determinant

equal to zero.

$$\begin{bmatrix} r_1 - b_1v - c_1w - 2p_1u & -b_1u & -c_1u \\ -a_2v & r_2 - a_2u - c_2w - 2p_2v & -c_2v \\ -a_3w & -b_3w & r_3 - a_3u - b_3v - 2p_3w \end{bmatrix}$$

The easiest equilibria to examine is  $(0,0,0)$ . The eigenvalues of this equilibrium are determined by

$$\begin{vmatrix} r_1 - \lambda & 0 & 0 \\ 0 & r_2 - \lambda & 0 \\ 0 & 0 & r_3 - \lambda \end{vmatrix} = (r_1 - \lambda)(r_2 - \lambda)(r_3 - \lambda) = 0$$

The three eigenvalues of this system are  $r_1, r_2$ , and  $r_3$ . Because all three eigenvalues are positive, all solutions move away from  $(0,0,0)$ , the equilibrium<sup>1</sup>. Thus, the equilibrium at  $(0,0,0)$  is unstable. An equilibrium of this type in three space is called a source. Figure 5.1 is a sketch of a typical source<sup>2</sup>.

The next equilibria we will examine are the three equilibria corresponding to the case where two of the species populations are zero. Without a loss of generality, we will study one of these three equilibria and the result will hold for the other two. Let us examine the equilibrium  $(\frac{r_1}{p_1}, 0, 0)$ . The eigenvalues of this system will be given by

$$\begin{vmatrix} -r_1 - \lambda & \frac{-b_1r_1}{p_1} & \frac{-c_1r_1}{p_1} \\ 0 & r_2 - \frac{a_2r_1}{p_1} - \lambda & 0 \\ 0 & 0 & r_3 - \frac{a_3r_1}{p_1} - \lambda \end{vmatrix} = 0, \text{ that is}$$

$$(-r_1 - \lambda)(r_2 - \frac{a_2r_1}{p_1} - \lambda)(r_3 - \frac{a_3r_1}{p_1} - \lambda) = 0$$

The eigenvalues of this system will be  $\lambda_1 = -r_1$ ,  $\lambda_2 = r_2 - \frac{a_2r_1}{p_1}$ , and  $\lambda_3 = r_3 - \frac{a_3r_1}{p_1}$ . The equilibrium under consideration will only be asymptotically stable when all three eigenvalues are negative. The first eigenvalue  $\lambda_1$  will always be negative. The second and third eigenvalues, which are clearly real (no imaginary part), will be negative if and only if

$$\frac{r_2}{r_1} < \frac{a_2}{p_1}, \quad \frac{r_3}{a_3} < \frac{r_1}{p_1}$$

<sup>1</sup>This can be developed from Boyce and DiPrima pgs 350 - 356 and 365 - 369

<sup>2</sup>Hubbard, John, and Beverly West. MacMath. New York: Springer-Verlag 1992. pg 69.

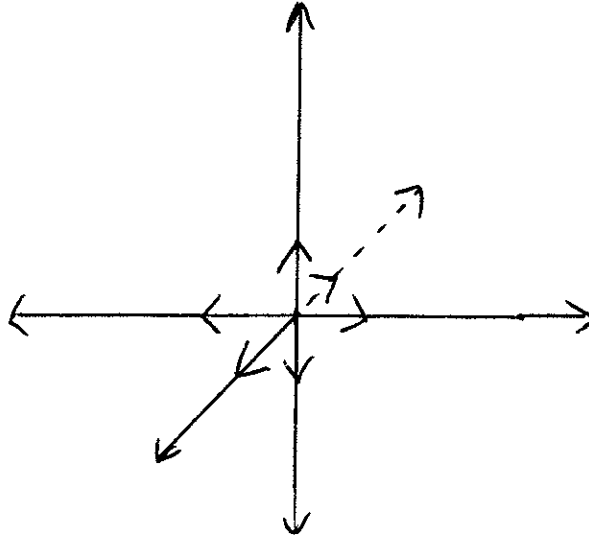


Figure 5.1: Trajectories near a source in a three dimensional system.

If the above is the case, then from chapter two we can see that the species  $X$  and  $Y$  cannot coexist in a closed system of just those two species. This is a direct consequence of the first inequality above. Similarly, by the second inequality,  $X$  and  $Z$  cannot coexist in a closed two species environment.

All of this really makes sense in a biological way. A species  $X$  is very competitive with the two other species in its environment. The other two species have relatively small populations, and the species under consideration,  $X$ , has a relatively large population. Under these conditions, species  $X$  should dominate and force the other species to become extinct. This is exactly the situation we have just analyzed above.

Now, let us return to the eigenvalues and make another assumption. Assume the pairs of species  $X$  and  $Y$ , and  $X$  and  $Z$  can coexist. By the previous inequalities, it follows that  $\lambda_2$  and  $\lambda_3$  are positive at this equilib-

rium.. A general solution of a three dimensional system could look like<sup>3</sup>

$$\begin{bmatrix} X \\ Y \\ Z \end{bmatrix} = k_1 \Lambda_1 e^{\lambda_1 t} + k_2 \Lambda_2 e^{\lambda_2 t} + k_3 \Lambda_3 e^{\lambda_3 t} \quad (5.2)$$

In the general solution, each  $c_j$  is given by the initial population, and  $\Lambda_j$  is the eigenvector corresponding to  $\lambda_j$ . The three eigenvectors in the general solution are linearly independent<sup>4</sup>. As time increases, the value of the first part of the general solution will approach zero as a result of the negative eigenvalue exponent. Thus, the trajectories of the system will approach the plane defined by the other two eigenvectors  $\Lambda_2$  and  $\Lambda_3$ . Because the eigenvalue exponents  $\lambda_2$  and  $\lambda_3$  are positive, as time increases the solutions will move further from the equilibrium along the plane defined by their corresponding eigenvectors. An equilibrium of this nature is called a 1 to 2, or 1-2, unstable saddle<sup>5</sup>. Figure 5.2 is a sketch of one such saddle with a few trajectories.

We have just studied the nature of the equilibria corresponding to the carrying capacities of each species. Next, we examine the equilibria corresponding to the points where two of the species may coexist and one species is extinct. As in the previous discussion, without a loss of generality we will examine one such equilibrium and extend the result to all three equilibria of this nature.

The eigenvalues associated with the equilibrium

$$\left( \frac{-r_1 p_2 + b_1 r_2}{-p_1 p_2 + b_1 a_2}, \frac{-r_2 p_1 + a_2 r_1}{-p_1 p_2 + b_1 a_2}, 0 \right) = (S, T, 0)$$

are given by

$$\begin{vmatrix} r_1 - b_1 T - 2p_1 S - \lambda & -b_1 S & -c_1 S \\ -a_2 T & r_2 - a_2 S - 2p_2 T - \lambda & -c_2 T \\ 0 & 0 & r_3 - a_3 S - b_3 T - \lambda \end{vmatrix} = 0, \text{ or}$$

$$\begin{aligned} & (r_3 - a_3 S - b_3 T - \lambda) \\ & ((r_1 - b_1 T - 2p_1 S - \lambda)(r_2 - a_2 S - 2p_2 T - \lambda) - a_2 b_1 S T) = 0 \end{aligned}$$

<sup>3</sup>This is an extension of the results and work done in Boyce and DiPrima in chapters 9 and 7. An interested reader can study the material given there. However, because of space considerations, the results from the phase plane will not be extended into their three dimension analog here.

<sup>4</sup>Anton, Howard. Elementary Linear Algebra 5e. New York: Wiley 1973. pg 314.

<sup>5</sup>MacMath pg 69.

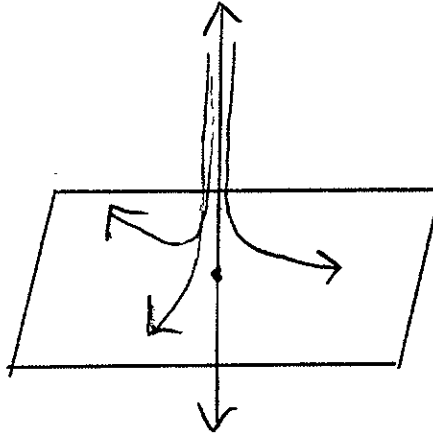


Figure 5.2: A 1-2 unstable saddle.

The second factor above on the second line is exactly the characteristic equation of the two species competitive system from chapter two. While we did not pursue the equation and eigenvalues in chapter two, our results in that chapter can be helpful here. The system in chapter two was asymptotically stable for a certain condition. Because that condition gave us asymptotic stability in chapter two, it also forced the roots of the characteristic equation of chapter two to be negative. The roots of that equation are the eigenvalues. Thus without solving this system any further, we have some results about its eigenvalues. The eigenvalues in the second factor will be negative if and only if the condition of chapter two holds for these two species. That is, in a two species closed system, species  $X$  and species  $Y$  will coexist. If the two species cannot coexist because of intense competition in their two species ecosystem, then their eigenvalues given in the above complicated determinant will be positive.

Still, we need to address the third eigenvalue given by setting the first expression in the above determinant equal to zero:

$$\lambda = r_3 - a_3S - b_3T$$

Clearly this eigenvalue will be some real number. Because we have assumed species  $X$  and  $Y$  have an equilibrium in the positive  $XY$  plane,  $S$  and  $T$

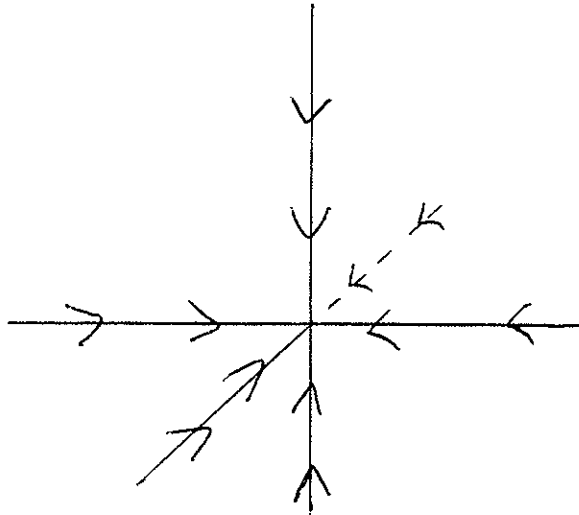


Figure 5.3: The asymptotically stable sink.

are positive numbers. The eigenvalue will be negative if either competitive parameter  $a_3$  or  $b_3$  is large enough. So, if the competition from species  $X$  or  $Y$  is too intense, the eigenvalue will be negative. If the competition is relatively mild, the eigenvalue will be positive.

Finally, some conclusion to this examination is needed. If two species can coexist together and offer strong competition to the third species, the equilibrium will have three negative eigenvalues. In this case, the equilibrium is asymptotically stable. Such an equilibrium in three dimensions, space, is called a sink. An example of a sink<sup>6</sup> is given in figure 5.3.

If the two species coexist and offer mild resistance to the third species, the final eigenvalue will be positive. From our general solution 5.2, we can see the single positive eigenvalue will force solutions to follow the path described by its corresponding eigenvector. The influence of the other eigenvectors will diminish as time increases as a result of their negative eigenvalue exponents. An equilibrium of this nature is called 2-1 unstable saddle. An example of a 2-1 unstable saddle equilibrium<sup>7</sup> is given in figure 5.4.

If the two species with populations in the equilibrium cannot coexist in

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<sup>6</sup>MacMath pg 69.

<sup>7</sup>MacMath pg 69.

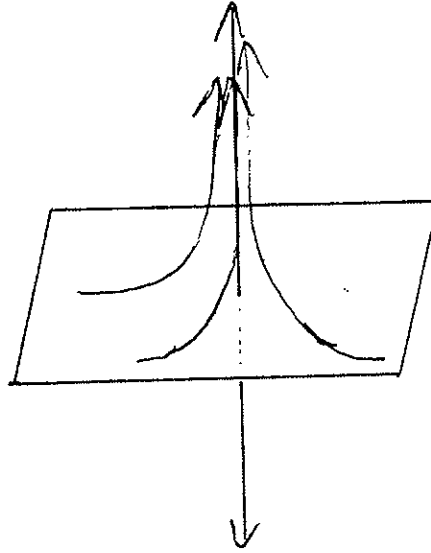


Figure 5.4: A sketch of a typical 2-1 unstable saddle.

their two species closed system, and compete strongly with the third species, all three eigenvalues will be positive. The equilibrium is then a source as in figure 5.1. If the competition is mild, then the third eigenvalue becomes negative. This equilibrium then is the unstable 1-2 saddle from figure 5.2.

In this section of this chapter we have examined all equilibria except the equilibrium  $E$ . Because of the complex nature of this equilibrium, a simple eigenvalue analysis does not exist. To develop some ideas about the nature of this equilibrium, we turn to an experimental process in the next section of this chapter.

## 5.2 Exploring the Model



The purpose of this section is to explore examples of closed three species competitive systems. This section relies heavily on the Runge-Kutta method of numerical approximation of solutions. The graphs and figures were produced using MacMath software<sup>8</sup>. The values of the growth rate parameters,  $r_j$ , and the environmental capacity parameters,  $p_j$ , have been standardized to one. Because of the small significance of these parameters with regard to stability, all examples focus on the roles of the other parameters.

The goal of this section is to form a conjecture, based on intuition and examples, with a conclusion of coexistence for all three species at some equilibrium. To pursue this, we begin with an example of a system where all three species coexist at  $E$  their asymptotically stable equilibrium<sup>9</sup>. Figure 5.5 is an example of such a system. The equations for this system are

$$\begin{aligned}\frac{dX}{dt} &= X - .5XY - .5XZ - X^2 \\ \frac{dY}{dt} &= Y - .5XY - .5YZ - Y^2 \\ \frac{dZ}{dt} &= Z - .5XZ - .5YZ - Z^2\end{aligned}$$

This system is very nicely balanced. The equations are all very similar. Notice the parameters of competition in each equation above. Each species rate is decreased by competitive factors with coefficients of .5. Because competition occurs between pairs of species, let us examine the competition between any of the two in the above system, say  $X$  and  $Y$ . The competitive measure or product of the competition factors coefficients,  $(.5)(.5)$  in this example, is .25. The competitive measure can be compared to the product of each species' logistic parameter ( $p_j$  in section one of this chapter). The product of all logistic parameters in this section of chapter two will be one, as in this example. Because the competitive measure, .25 is less than the logistic product, one, the competition between  $X$  and  $Y$  is said to be relatively weak or mild. If the competitive measure were greater than one, then the competition could be described as relatively strong, aggressive, or fierce.

Now notice the elegant rose-like graph of this system. All trajectories move toward the equilibrium  $E$  in the positive octant. The arrow marks on the trajectories indicate their direction of motion in all graphs in this section. Each species in this system behaves similarly. Over time each

<sup>8</sup>Hubbard, John, and Beverly West. MacMath 9.0 Computer software. Springer-Verlag, 1992. Macintosh, disk.

<sup>9</sup>This is the same equilibrium  $E$  defined in the previous section.

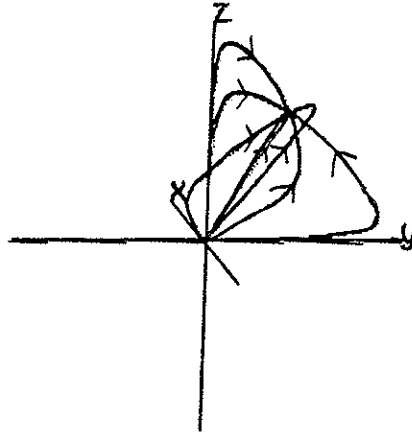


Figure 5.5: A system with all species coexisting at  $E$ .

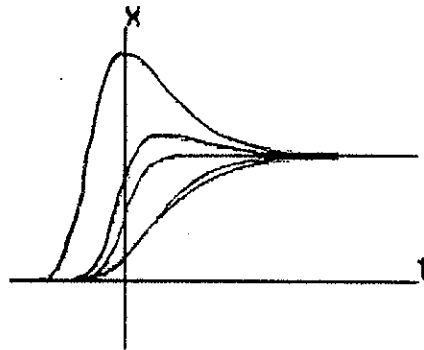


Figure 5.6: The population of a species over time.

species approaches a specific population. The  $X$  species is plotted versus time in figure 5.6. This pattern is typical for all three species of this system.

The equations above are so balanced that even in the absence of any of the three species the other two could coexist. Each pair of species' parameters fits the requirements of chapter two for coexistence between two species in a closed environment. This is our working definition of coexisting pairs. The systems examined in this chapter can be reduced to their three systems of two species by letting each species' population, one at a time, be zero.

This brings us to a logical way to examine this system. Now that we have a coexisting example with some property, each pair coexists, let us slowly break this down and study the results. First, we will examine systems where one pair of species does not coexist. Then, we will look at systems with two noncoexisting pairs. Finally, we will look at systems where no two species can coexist.

After examining many examples of systems where a single parameter caused the competitive measure to be greater than one in one pair of species, it seemed that coexistence at  $E$  was not possible. One such system is

$$\begin{aligned}\frac{dX}{dt} &= X - .5XY - 4XZ - X^2 \\ \frac{dY}{dt} &= Y - .5XY - .5YZ - Y^2 \\ \frac{dZ}{dt} &= Z - .5XZ - .5YZ - Z^2\end{aligned}$$

The graph of this system with a few trajectories can be found in figure 5.7. The species in this system coexist when the species  $X$  is extinct.

Two species will also fail to coexist if they both compete too aggressively with each other. The following system, graphed in figure 5.8, is a typical system of this nature. Note that the system has a point of coexistence<sup>10</sup> only when either species  $X$  or  $Y$  is extinct. The initial population of the system determines which of the aggressive competitors,  $X$  or  $Y$ , will survive.

$$\begin{aligned}\frac{dX}{dt} &= X - 1.3XY - .5XZ - X^2 \\ \frac{dY}{dt} &= Y - 3XY - .5YZ - Y^2 \\ \frac{dZ}{dt} &= Z - .5XZ - .5YZ - Z^2\end{aligned}$$

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<sup>10</sup>This is a shorthand way to describe an asymptotically stable equilibrium.

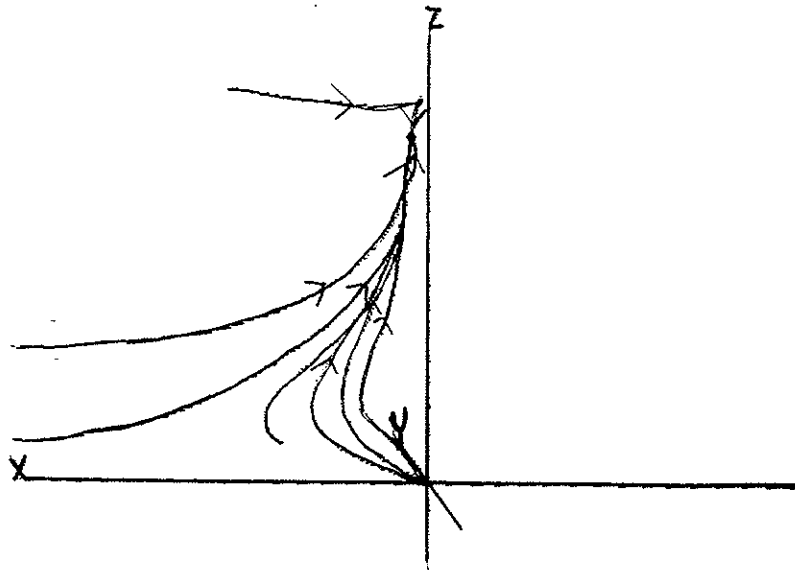


Figure 5.7: A system with one parameter causing one pair to not coexist.

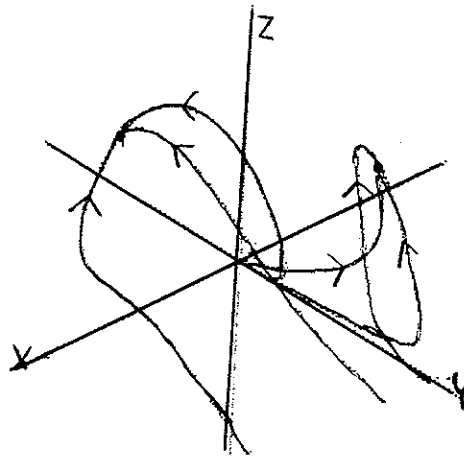


Figure 5.8: An example of two fiercely competing competitors.

So far, we have looked at two examples of systems where one pair of species does not coexist. The results of these examples typified the many other examples of this nature examined. If one pair of species will not coexist, then there is no point of coexistence where all three species have nonzero populations.

Next, we turn to the case where two pairs of species fail to coexist. Let us begin with the system

$$\begin{aligned}\frac{dX}{dt} &= X - 4XY - 3XZ - X^2 \\ \frac{dY}{dt} &= Y - .5XY - .5YZ - Y^2 \\ \frac{dZ}{dt} &= Z - .5XZ - .5YZ - Z^2\end{aligned}$$

The  $X$  species cannot coexist with either of the other two species in a two species system. As a result, the point of coexistence in the graph of this system, figure 5.9, has the population of  $X$  as zero. Species  $X$  cannot endure the competition and dies. Even in the examples where  $X$  offered heavy competition to one of the other competitors, the results were no different.

A similar result happens in systems where one species competes too aggressively with the second species, and the second species competes too aggressively with the third species. The second species is forced to extinction by the first species, as in the first system examined in this section. When the second species becomes extinct, the remaining two species' populations, which can coexist together, move to their point of coexistence.

The next system is an example where one species competes too aggressively with each of the other two. The point of coexistence of this system occurs at the equilibrium corresponding to this ultimate competitors maximum environmental capacity. The example of this type of system given below is graphed in figure 5.10.

$$\begin{aligned}\frac{dX}{dt} &= X - .5XY - 3XZ - X^2 \\ \frac{dY}{dt} &= Y - .5XY - 3YZ - Y^2 \\ \frac{dZ}{dt} &= Z - .5XZ - .5YZ - Z^2\end{aligned}$$

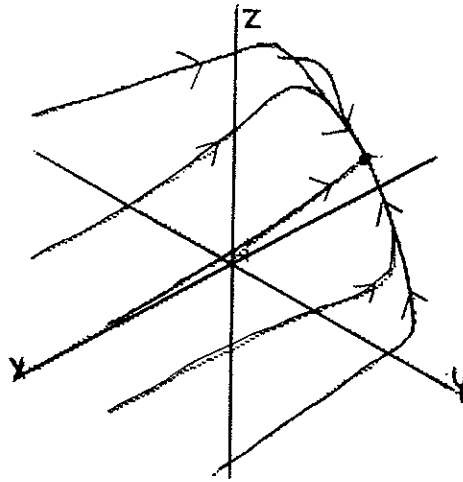


Figure 5.9: Two species compete aggressively with the third species.

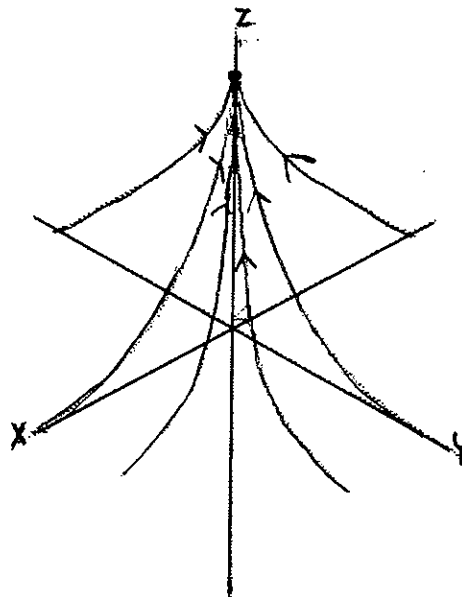


Figure 5.10: The ultimate competitor.

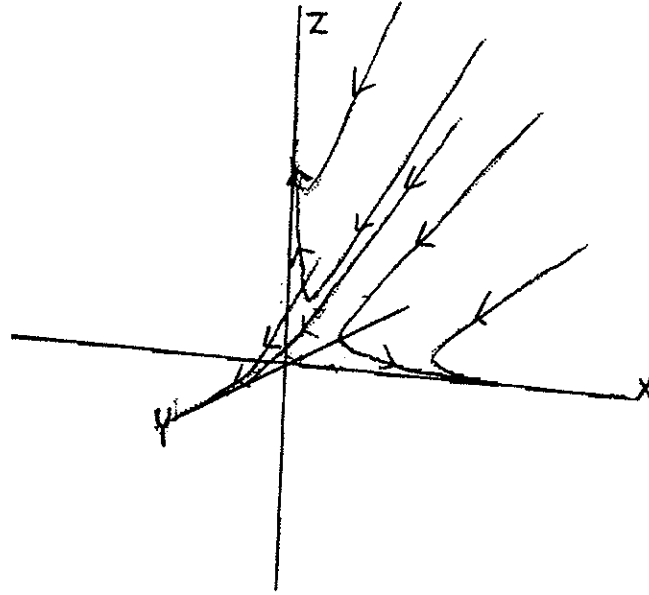


Figure 5.11: A system of aggressive competitors.

Now that we have taken a fair look at systems where two pairs of species do not coexist, let us look into the cases where all three species do not coexist. The first and most obvious case occurs when all three species compete aggressively with each other. An example of this type of system is:

$$\begin{aligned}\frac{dX}{dt} &= X - 4XY - 4XZ - X^2 \\ \frac{dY}{dt} &= Y - 4XY - 4YZ - Y^2 \\ \frac{dZ}{dt} &= Z - 4XZ - 4YZ - Z^2\end{aligned}$$

In this system graphed in figure 5.11, all three logistic equilibria are asymptotically stable. These are the three equilibria of the system corresponding to each species maximum population if no competitors were present. The equilibrium a particular solution approaches is determined by the initial population of the system. The species given the slightest advantage is the only one that survives the competition.

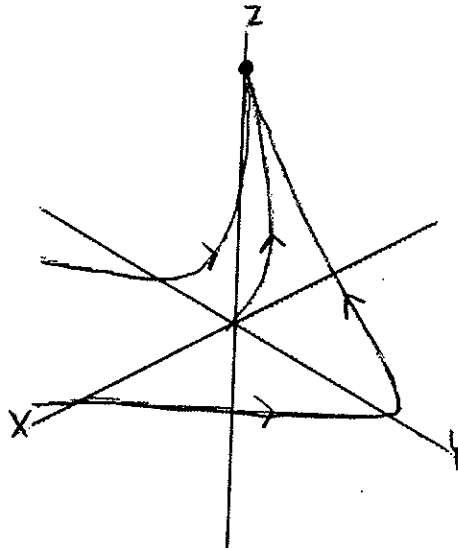


Figure 5.12: The strongest of three aggressive competitors survives.

This result extends into systems without such intense competition. For example,

$$\begin{aligned}\frac{dX}{dt} &= X - 2.1XY - 3XZ - X^2 \\ \frac{dY}{dt} &= Y - .5XY - 2.1YZ - Y^2 \\ \frac{dZ}{dt} &= Z - 2.1XZ - .5YZ - Z^2\end{aligned}$$

In this system, the weakest species,  $X$ , is forced into extinction quite rapidly. At the same time, the  $Y$  species is slowly dominated by the  $Z$  species. Again, in very aggressive competition, the strongest species is the one which will dominate. The graph of this system can be found in figure 5.12.

The final example in this section is the most interesting. Let three species compete in a cyclical pattern. One species dominates the second. The second species dominates the third, and the third dominates the first. A system of this type is



$$\begin{aligned}\frac{dX}{dt} &= X - 2.1XY - .5XZ - X^2 \\ \frac{dY}{dt} &= Y - .5XY - 2.1YZ - Y^2 \\ \frac{dZ}{dt} &= Z - 2.1XZ - .5YZ - Z^2\end{aligned}$$

The result is a limit cycle<sup>11</sup>. The trajectories of the system approach some cyclical trajectory instead of a point. In figure 5.13, notice how the trajectory moves out toward a triangular limit cycle. Also included with the graph of this figure is the graph of the  $X$  species population over time. Each species of this system exhibits the behavior of this second graph. The populations oscillate between their maximums and zero with an increasing period.

After exploring several examples and developing an intuitive feel for these types of systems, a conjecture is present. The only examples with a point of coexistence for all three species occurred when each pair of species was able to coexist. Proving this is a sufficient condition for stability is left to the next section of this chapter. Unfortunately, the interesting limit cycle example must be set aside. The focus of this work is to find conditions for asymptotically stable equilibria.

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<sup>11</sup>The interested reader can find more information on limit cycles in Boyce and DiPrima Ch 9.7.

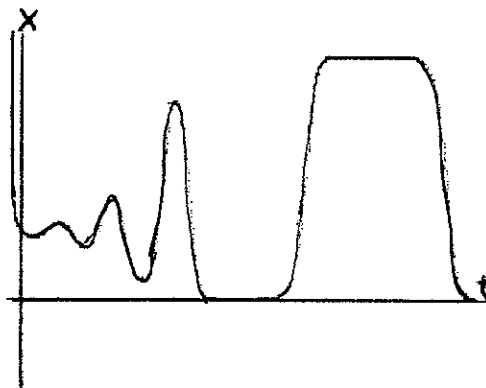
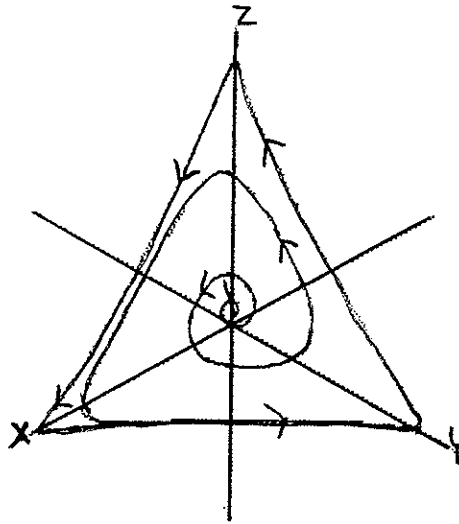


Figure 5.13: A system with a limit cycle.

### **5.3 Conjectures and Theorems**

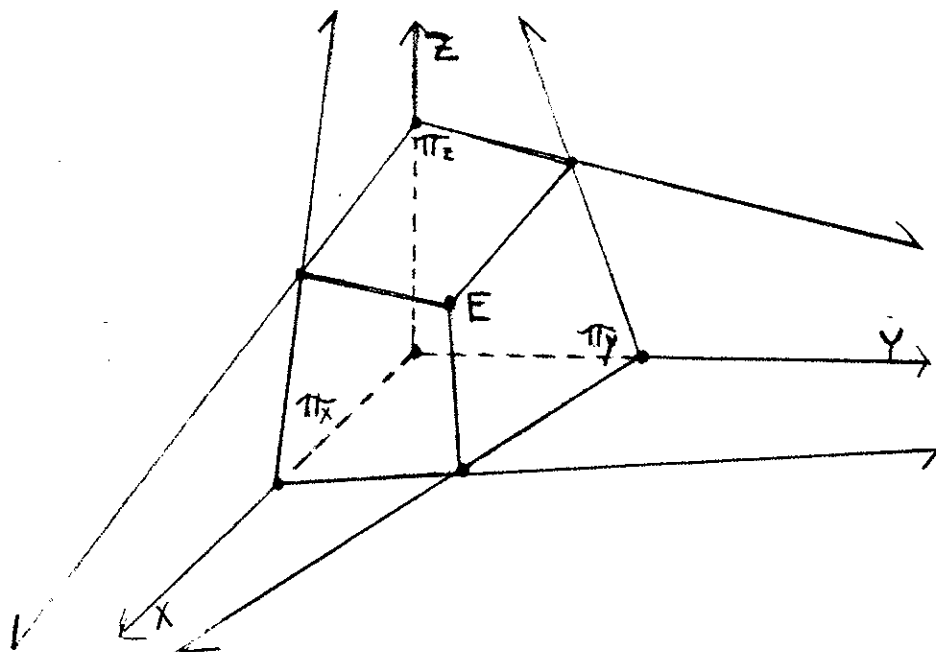


Figure 5.14: The space bounded by the isoplanes.

Finally, we return our attention to the equilibrium  $E$ . In this section we attempt to prove  $E$  is at least asymptotically stable, given all three pairs of the three species would coexist in closed two species ecosystems. This section is dominated by the geometry of a three dimensional figure. The figure is bounded by the three isoplanes defined in section one of this chapter and the coordinate planes of the three dimensional space. The equilibrium  $E$  is the intersection of the three isoplanes. This figure can be seen in figure 5.14.

This section is divided into three parts. In the first part, we will look at the figure described by figure 5.14, the ecospace, and prove that the space must be convex. Second, we will argue that the equilibrium  $E$  is the only candidate for stability or asymptotic stability for the system of three competing species. Finally, based on an assumption, we will show that  $E$  is at least stable.

However, before going further, let us present the conjecture we will ex-

plote.

**Conjecture: 1** *If three species existing in the closed hypothetical model of this chapter alll coexist in pairs as described in chapter two, then the equilibrium  $E$  is at least stable.*

From chapter two, the condition or hypothesis of coexisting pairs is:

$$\frac{p_2}{b_1} > \frac{r_2}{r_1} > \frac{a_2}{p_1}, \text{ and } \frac{p_3}{c_1} > \frac{r_3}{r_1} > \frac{a_3}{p_1}, \text{ and } \frac{p_2}{b_3} > \frac{r_2}{r_3} > \frac{c_2}{p_3} \quad (5.3)$$

As a result of the above hypothesis, the ecospace in figure 5.14 is the region in the first octant that lies below each of the isoplanes and above each of the coordinate planes. A point is considered to be above an isoplane if the line segment from the origin to the point intersects the isoplane. If this line segment fails to intersect the isoplane, then the point is below the isoplane. Another way to define this space is the set of

$$\begin{aligned} & r_1 - b_1Y - c_1Z - p_1X > 0 \\ (x, y, z) \text{ such that } & r_2 - a_2X - c_2Z - p_2Y > 0 \\ & r_3 - a_3X - b_3Y - p_3Z > 0 \end{aligned}$$

Without a loss of generality, we will examine the space above the coordinate planes and below just one isoplane, the  $X$  isoplane,  $\Pi_x$ . Then, we will apply the information provided by this study to all three spaces defined by the coordinate axes and an isoplane. We will examine the ecospace as the intersection of these three spaces.

**Theorem: 1** *The space bounded by the coordinate planes and the isoplanes generated by the model for three competing species in one closed ecospace is convex.*

**Proof:** Recall from earlier work that the equation for the  $X$  isoplane,  $\Pi_x$ , is  $r_1 - b_1Y - c_1Z - p_1X = 0$ . For  $\Pi_x$ , note that the value of  $x$  is zero when  $r_1 - b_1Y - c_1Z = 0$ . Similarly, the value of  $y$  is zero when  $r_1 - c_1Z - p_1X = 0$ , and  $z$  is zero when  $r_1 - b_1Y - p_1X = 0$ . These are the three lines where  $\Pi_x$  meets one of the coordinate axes. Also note, these three lines of intersection meet the coordinate axes at the points  $(\frac{r_1}{p_1}, 0, 0)$ ,  $(0, \frac{r_1}{b_1}, 0)$ , and  $(0, 0, \frac{r_1}{c_1})$ . Thus, the space bounded by the coordinate planes and  $\Pi_x$  is closed. Figure 5.15 is a representation of this figure.

Now we proceed to show the space in figure 5.15 is a convex space. Let  $N$  and  $M$  be any two points in the space bounded by  $\Pi_x$  as in figure 5.15.

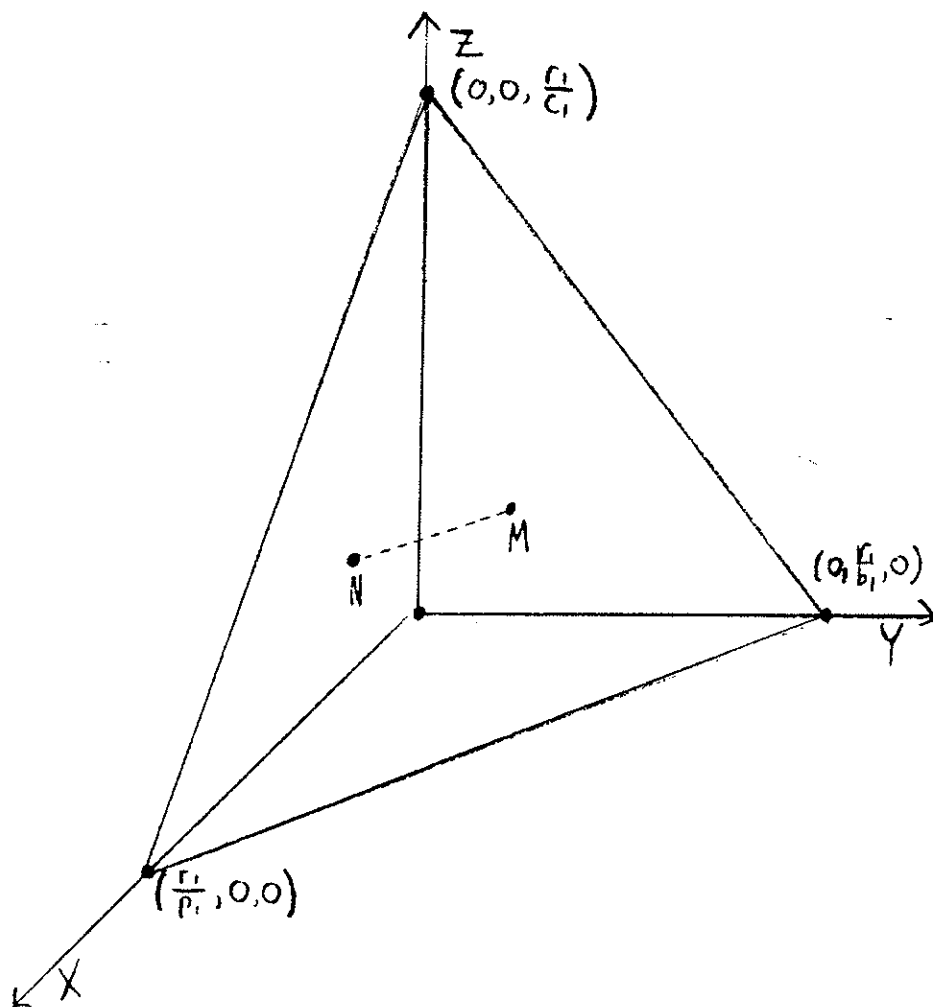


Figure 5.15: The space bounded by the coordinate planes and  $\Pi_x$ .

Construct the line segment  $\overline{NM}$ . Because the points  $N$  and  $M$  are on the same side of the plane  $\Pi_x$ , the line segment  $\overline{NM}$  must also be on the same side of that plane. Also, since  $N$  and  $M$  are in the first quadrant, the points on  $\overline{NM}$  must also be in the first quadrant. Thus, for any two points in the space we are considering, the line segment between these points is also in the space. Because this is always the case, the space bounded by  $\Pi_x$  and the coordinate planes will be convex.

By similar proof, the space bounded by either  $\Pi_y$  or  $\Pi_z$  and the coordinate planes will also be convex. The intersection of a finite number of convex spaces must be convex. Thus, the ecospace in figure 5.14 must be a convex space.  $\Delta$

It is also worth noting that the derivative in the space bounded by the coordinate planes and the isoplane will be positive. Thus, in the intersection of all of these spaces, the ecospace, all the derivatives  $\frac{dX}{dt}$ ,  $\frac{dY}{dt}$ , and  $\frac{dZ}{dt}$  will be positive.

Now we move into the second part of this section of chapter five.

**Theorem: 2** *Given the conditions of the hypothesis 5.3 and the convexity of the ecospace, the only equilibrium with the potential to be either stable or asymptotically stable is  $E$ .*

**Proof:** From the work of section one, we know the equilibria  $(0,0,0)$ , and those corresponding to each species environmental carrying capacity are already eliminated.

It seems reasonable to assume a biological system and the model we are studying cannot have populations growing infinitely large. In a closed environment there are a limited amount of resources. There exist parameters in the system of this chapter limiting each species population as limited resources would. Thus, no population in our system should grow infinitely large. The populations must have either some stable equilibrium to cycle about or an asymptotically stable equilibrium (point of coexistence) to approach. The only possible equilibria with the potential for filling this requirement for the system are  $E$  and the equilibria corresponding to points of pairwise coexistence. The points of pairwise coexistence have the form  $(A, B, 0)$ ,  $(C, 0, D)$ , and  $(0, P, Q)$ , where the values of  $A, B, C, D, P$ , and  $Q$  are determined from the same equilibria in section one of this chapter.

Without a loss of generality, we will examine one of the three similar equilibria above and extend the results of our study to the other two. Let us choose  $(A, B, 0)$ . From our work in section one, we know none of the

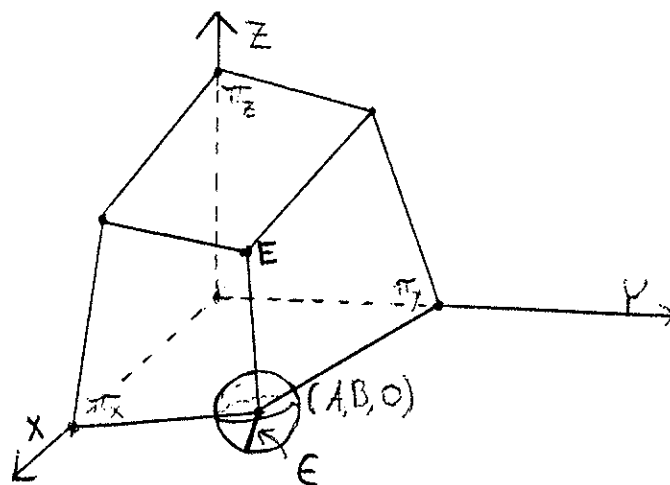


Figure 5.16: The boundary point  $(A, B, 0)$  with interval  $\epsilon$ .

eigenvalues at this equilibrium are imaginary. Thus, the only stability to consider at  $(A, B, 0)$  is asymptotic stability.

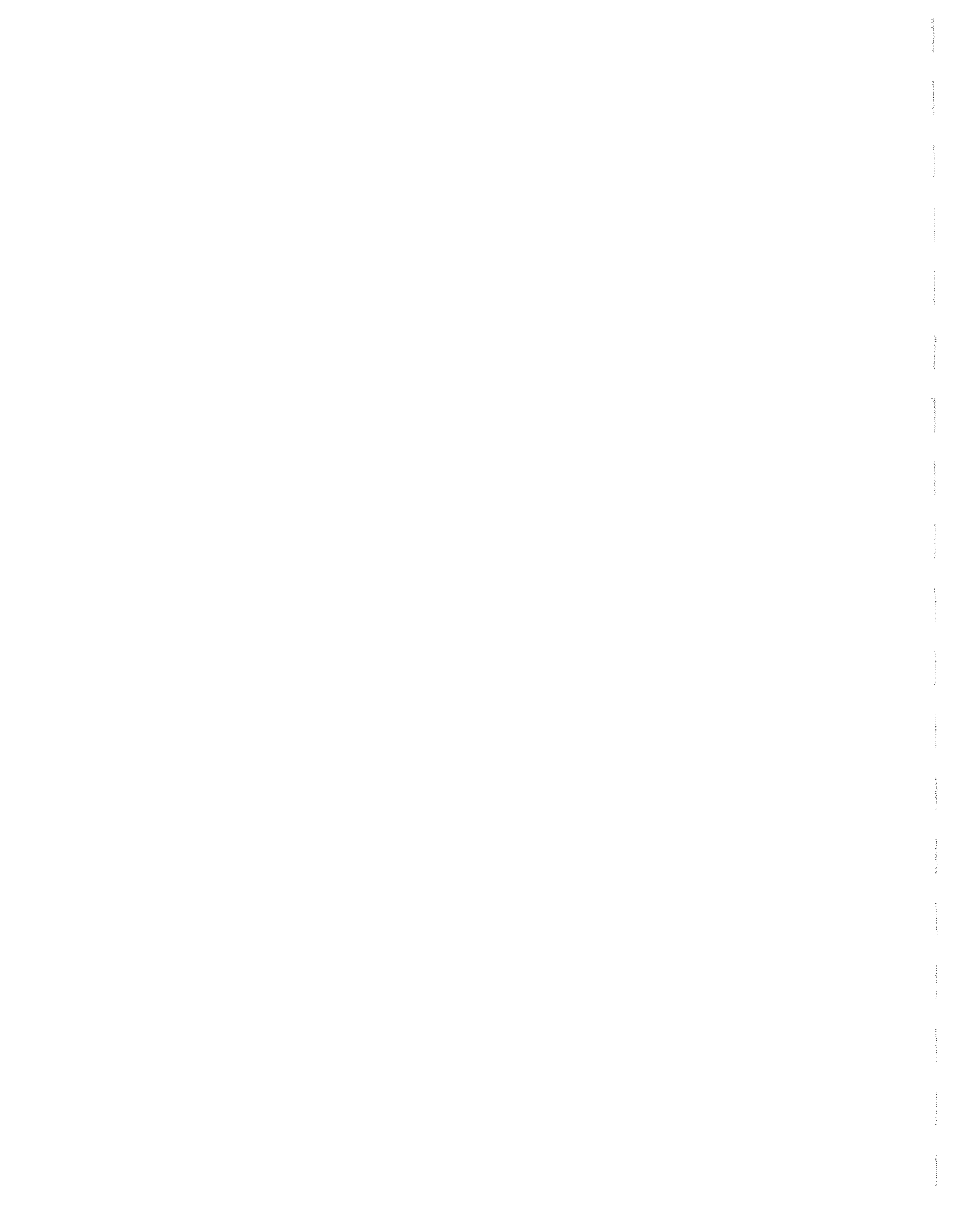
Assume the population of the system is asymptotically stable at  $(A, B, 0)$ . Then all species populations must approach this equilibrium. In particular, because we assume our initial population gave all species some population, it must be the case that  $\frac{dZ}{dt} < 0$  in some ball about  $(A, B, 0)$ . If this is the case, and there exists some population of  $Z$ , then it must be true that for some open ball<sup>12</sup> about  $(A, B, 0)$  we have  $r_3 - a_3X - b_3Y - p_3Z < 0$ . If this is the case, then this interval about the equilibrium must be outside of the ecospace. Assume this interval is the set of all points within a small distance  $\epsilon$  of  $(A, B, 0)$ . Figure 5.16 is a representation of this situation.

Now, recall that  $(A, B, 0)$  is in the coordinate plane  $z = 0$  and is the intersection of this coordinate plane and the two isoplanes  $\Pi_x$  and  $\Pi_y$ . Because these planes form part of the boundary of the ecospace their intersection must also be a boundary point of the ecospace. Let  $D$  be a point a distance of  $\frac{\epsilon}{2}$  from the boundary point  $(A, B, 0)$  and in the ecospace. Then at  $D$  all derivatives must be positive.

Now we have found a contradiction. The point  $D$  is in the interval about  $(A, B, 0)$  where the derivative  $\frac{dZ}{dt}$  is negative. Also, this derivative must be positive at the same time. This is a contradiction. Because the assumption of asymptotic stability led to a contradiction, this assumption must be false.

<sup>12</sup>The open ball is the points contained inside the sphere of radius  $\epsilon$  about  $(A, B, 0)$ .





Thus, since  $(A, B, 0)$  is not stable either, the equilibrium must be unstable.

We have shown that the only equilibrium that can be asymptotically stable or stable in our system of three competitors, where each pair of competitors coexists together, is  $E$ . Also, we have argued that there must be some equilibrium in the system that is stable or asymptotically stable. By the process of elimination,  $E$  must be asymptotically stable or stable.  $\Delta$

While we have a fair argument, it is built on an assumption that there must be some equilibrium. Because this assumption is not proven, the argument above does not prove our initial conjecture. Unfortunately, I have been unable to remove this assumption. We will have to keep the assumption in the hypothesis of the theorem. The final argument of this chapter cannot be taken as a proof of the conjecture either. While we will develop its assumption carefully to increase its plausibility, it still remains an assumption.

In figure 5.17 we have divided the positive octant into eight partitions using three planes. To simplify the construction and provide better intuition, the planes have been constructed in a fashion forming a cube in the back corner of the first octant with the origin  $(0, 0, 0)$  as one of its vertices<sup>13</sup>. Each of these planes divides this space just as the isoplanes divide the positive octant. Using figure 5.17, let us label each of these partitions. Let each partition be labeled by  $P_{ijk}$ . Let  $i = 0$  if the partition is in the back part of the figure, below  $\Pi_x$ , and 1 if the partition is in the front or above  $\Pi_x$ . Let  $j = 0$  if the partition is in the left part of the figure below  $\Pi_y$  and 1 if it is in the right part above  $\Pi_y$ . Let  $k = 0$  if the partition is in the bottom portion of the figure below  $\Pi_z$  and 1 if it is the upper portion above  $\Pi_z$ . Figure 5.17 may clarify these labels.

With space partitioned in this way let us look at the derivatives of the competitive system in each partition. Recall a positive derivative of a species implies the population of a species is increasing and a negative derivative implies the population is decreasing. Table 5.1 is a summary of the population behavior from the nature of the derivative in each quadrant.

From table 5.1 and figure 5.17 it appears that all trajectories approach the equilibrium  $E$  as we wish. The figure and table do not form a proof, but they do provide us with the insight we need for a proof. It seems quite logical to assume, based on the figure and table, that the trajectories of the system must approach all three isoplanes as time increases. This is the

<sup>13</sup>The reader is encouraged to try making constructions varying from this simple one. So long as the partition corresponding to the ecospace (the back corner) is convex the results will be the same.

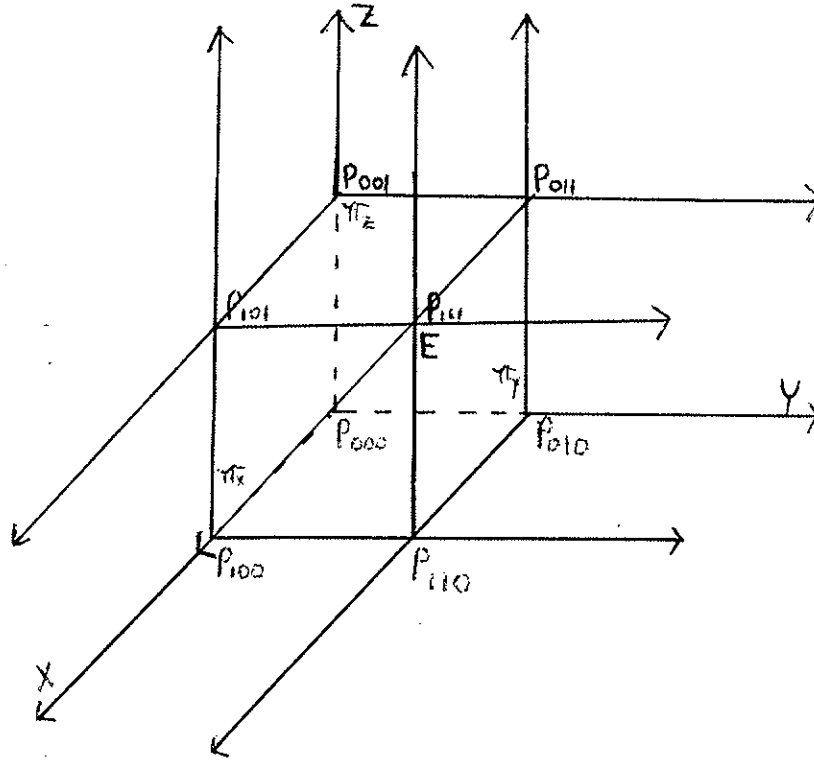


Figure 5.17: Partitioning the positive octant

| <i>partition</i> | <i>X population</i> | <i>Y population</i> | <i>Z population</i> |
|------------------|---------------------|---------------------|---------------------|
| $P_{000}$        | increasing          | increasing          | increasing          |
| $P_{001}$        | increasing          | increasing          | decreasing          |
| $P_{010}$        | increasing          | decreasing          | increasing          |
| $P_{011}$        | increasing          | decreasing          | decreasing          |
| $P_{100}$        | decreasing          | increasing          | increasing          |
| $P_{101}$        | decreasing          | increasing          | decreasing          |
| $P_{110}$        | decreasing          | decreasing          | increasing          |
| $P_{111}$        | decreasing          | decreasing          | decreasing          |

Table 5.1: Population change in each partition.

assumption we shall make in the following argument.

**Theorem: 3** *If three species exist in a closed ecosystem and competitors are following the system model 5.2 and if each pair of species follows the condition or hypothesis 5.3 and coexists in their closed two species ecosystem, then the equilibrium  $E$  is at least a stable equilibrium and may be asymptotically stable provided trajectories approach all isoplanes.*

**Proof:** From previous work, we know there exists a convex ecospace ( $P_{000}$  in figure 5.17) defined by a set of

$$\begin{aligned} & r_1 - b_1Y - c_1Z - p_1X > 0 \\ (x, y, z) \text{ such that } & r_2 - a_2X - c_2Z - p_2Y > 0 \\ & r_3 - a_3X - b_3Y - p_3Z > 0 \end{aligned}$$

Note, for an isoplane in general, if a point lies above the isoplane then the appropriate coordinate of the trajectory is decreasing. For example, if  $S = (x_1, y_1, z_1)$  is above  $\Pi_x$ , then  $r_1 - b_1Y - c_1Z - p_1X < 0$  and  $\frac{dX}{dt} < 0$ . Thus, the x-coordinate  $x_1$  must be decreasing. Similarly if  $S$  is below  $\Pi_x$  then  $x_1$  is increasing. Therefore, the x-coordinate of our solution is changing in a way which forces the trajectory to approach  $\Pi_x$ , where the derivative  $\frac{dX}{dt} = 0$  and the x-coordinate will no longer change.

This argument can be applied to the other isoplanes as well. This is our basis for the assumption introduced earlier. Now, let us assume trajectories of the system will approach each isoplane. Let  $S$  be any point in the positive octant. To show  $E$  is at least stable, we must only show the trajectory containing  $S$ ,  $S(t)$ , cannot move further away from  $E$ . By the existence and uniqueness theorems<sup>14</sup> we know  $S$  must have some trajectory passing through it.

First, note that the trajectory from our initial population  $S$ ,  $S(t)$ , could approach and even intersect an isoplane. However,  $S(t)$  cannot pass into a different partition or it would move away from some isoplane. Thus,  $S(t)$  is restricted to one partition of the positive octant.

Now we assume  $S(t)$  moves away from  $E$  and look for a contradiction. In particular, we hope to show  $S(t)$  must be getting further from some isoplane.

For some time  $t_1$ , let  $S = S(t_1)$  be a point in the ecospace a small distance from  $E$ . This distance is  $d(S(t_1), E) = d$ . The position of  $S(t)$  at time  $t$  is given by  $S(t) = (x(t), y(t), z(t))$ . At a time  $t_2 > t_1$  the position

<sup>14</sup>Boyce and DiPrima pg 321

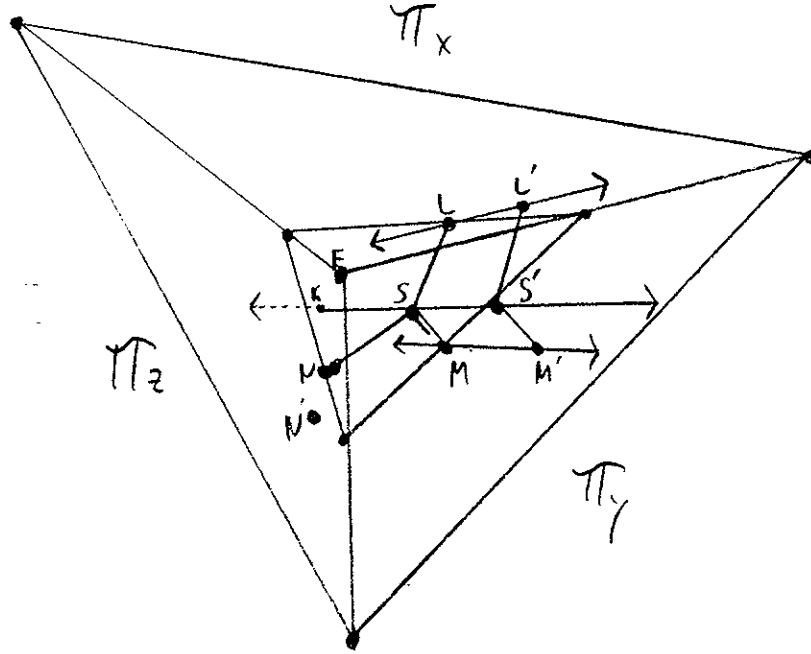
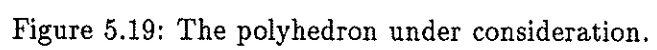


Figure 5.18: Proof by contradiction.

of  $S(t)$  has moved to  $S' = S(t_2) = (x(t_2), y(t_2), z(t_2))$ . Denote the distance from  $E$  to  $S(t_2)$  as  $d(S(t_2), E) = d'$ . For our contradiction, assume  $d' > d$ .

Let  $L$  and  $L'$  be points in  $\Pi_x$  such that  $\overline{SL}$  and  $\overline{S'L'}$  are normals to the plane. Let  $M$  and  $M'$  be points in  $\Pi_y$  such that  $\overline{SM}$  and  $\overline{S'M'}$  are normals to the plane. Also, let  $N$  and  $N'$  be points in  $\Pi_z$  such that  $\overline{SN}$  and  $\overline{S'N'}$  are normals to the plane. For the rest of this proof it may be helpful to refer to figure 5.18.

In accordance with our assumption, let us assume the distance of  $S'$  to two of the isoplanes is unchanged or less than the distances from  $S$  to each of these two isoplanes. Without a loss of generality, let us assume  $d(S, L) \geq d(S', L')$  and  $d(S, M) \geq d(S', M')$ . That is the trajectory under inspection moves further from  $E$  but no further from two of the isoplanes. Now we look for  $d(S, N) < d(S', N')$ , or that the trajectory moves away from the third isoplane,  $\Pi_z$ .



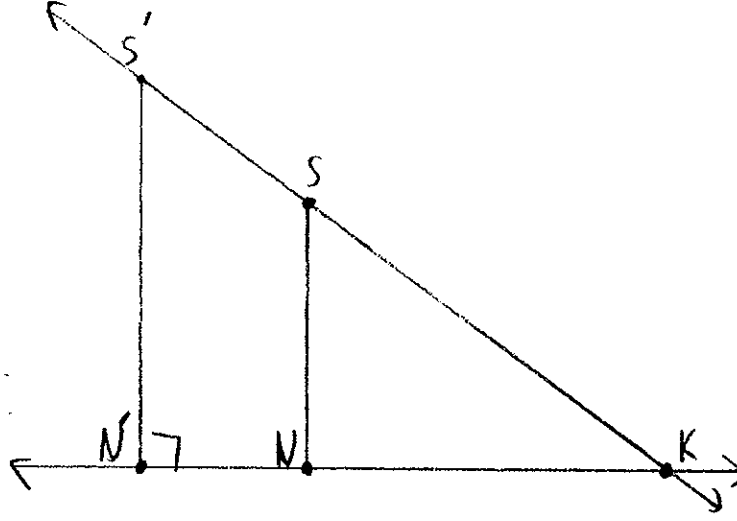


Figure 5.20: Similar triangles

Now construct  $\overleftrightarrow{SS'}$ ,  $\overleftrightarrow{LL'}$  and  $\overleftrightarrow{MM'}$ . Because  $d(S, L) \geq d(S', L')$  and  $d(S, M) \geq d(S', M')$ , if  $\overleftrightarrow{SS'}$  intersects with either  $\Pi_x$  or  $\Pi_y$ ,  $L'$  is between this intersection and  $L$  or  $M'$  is between this intersection and  $M$  on their respective lines. This follows directly from the nature of the two pairs of parallel normals:  $\overleftrightarrow{SL}$  and  $\overleftrightarrow{S'L'}$ , and  $\overleftrightarrow{SM}$  and  $\overleftrightarrow{S'M'}$ .

Now refer to figure 5.18 and note the polyhedron in figure 5.19 with faces  $\Pi_x, \Pi_y, \Pi_z$ , and plane  $LMN$ . The line  $\overleftrightarrow{SS'}$  enters this polyhedron through the base plane  $LMN$  and must exit or intersect one of the other faces. If this line intersects either  $\Pi_x$  or  $\Pi_y$ , this intersection occurs where these isoplanes are not faces of the polyhedron. Thus,  $\overleftrightarrow{SS'}$  must intersect and exit the polyhedron through a point  $K$  in  $\Pi_z$ .

We know the normals to the isoplane  $\Pi_z$ ,  $\overleftrightarrow{SN}$  and  $\overleftrightarrow{S'N'}$  must be parallel. Next, examine the similar triangles formed by these two normals,  $\overleftrightarrow{SS'}$ , and the line  $\overleftrightarrow{K'K}$  in  $\Pi_z$ . These four line segments or lines all contain two of the points  $S, C, S'$ , or  $C'$  and so must be coplanar. Refer to figure 5.20 to see a representation of this triangle.

Since  $d(D, S) < d(D, S')$ , it follows that  $\frac{d(D, S)}{d(D, S')} < 1$ . By the nature of similar triangles we know

$$\frac{d(D, S)}{d(D, S')} = \frac{d(S, C)}{d(S', C')} \text{ or, } \frac{d(S, C)}{d(S', C')} < 1$$

This simplifies to  $d(S, C) < d(S' C')$ . This is exactly the contradiction we were looking for. Thus, if a trajectory moves away from  $E$  it must move away from at least one isoplane. That is a contradiction with the assumption we made earlier about this system. Thus, no trajectory can move away from  $E$ , and  $E$  is at least a stable equilibrium and may be asymptotically stable.  $\Delta$

The argument above is based on an assumption that trajectories must approach all isoplanes. It seems that this follows from the convex ecospace, but at this time there is no proof of this. That is the weakness of this argument. Also, it would seem there should be an argument similar to the one constructed above forcing the equilibrium  $E$  to be asymptotically stable, but it has not been found either.

The results of this chapter are inconclusive. It would seem that the equilibrium  $E$  is at least stable. However, both proofs of this rely on assumptions which are not proven. The strength of the arguments is based on the amount of credibility one places on the assumptions.



## Chapter 6

# Models of Three Species: Two Systems

This chapter is an intuitive introduction to two closed ecosystems containing three species. In both parts the approach will be similar to the approach of the second section of chapter five. In the first part we will explore and make a conjecture about a model for ecosystems with two competitors and one predator. In the second part we will examine a model for systems with three biological levels. The first species will be the prey of the second species. The second species will also be the prey of the third species.

In this chapter we examine an ecosystem with two biological levels. The first level consists of two prey species. The second level consists of a single predator. We can make several assumptions that will lead us to a model of this type of ecosystem.

1. The two competing species follow the competitive model from chapter two.
2. The two competing species are prey. Each competitor or prey species' growth rate is decreased by an amount proportional to the product of the prey and predator populations. Thus, in the absence of the predator, the system reduces to the system from chapter two.
3. The predator follows the Lotka-Volterra model for predators. Without prey the predator dies. The growth rate of the predator is increased by an amount proportional to the product of the predator and prey populations.

Based on these assumptions, we can create the following model where  $X$  and  $Y$  are the competing prey and  $Z$  is the predator.

$$\begin{aligned}\frac{dX}{dt} &= r_1X - b_1XY - c_1XZ - p_1X^2 \\ \frac{dY}{dt} &= r_2Y - a_2XY - c_2YZ - p_2Y^2 \\ \frac{dZ}{dt} &= -r_3Z + a_3XZ + b_3YZ\end{aligned}\tag{6.1}$$

In the previous chapter, it seemed that the stability of the three species system depended upon the stability of each of the three pairs. However, because the predator only needs one of the two competitors for survival, only one of the prey must have the parameters capable of supporting the predator. Thus, we can form a conjecture.

**Conjecture: 2** *All three species of a hypothetical closed ecosystem following the model 6.1 will coexist if*

- *The two prey species will coexist as a pair as in chapter two.*
- *Either of the two prey species and the predator are capable of coexisting.*

In chapter five the reader became familiar with the terminology of pairwise coexistence of competitors. In review, recall that the predator and prey relationships in this model follow the modified Lotka-Volterra model of chapter four. According to this model, the predator  $Z$  and prey  $X$  will coexist if  $\frac{r_1}{p_1} > \frac{r_2}{a_3}$ . The predator will coexist with the prey  $Y$  if  $\frac{r_2}{p_2} > \frac{r_3}{b_3}$ .

As in section two of chapter five we will set the growth rates and the carrying capacities of the populations to one and focus on the parameters of interaction between the species. As a result, the competitors will coexist when  $a_2 < 1$  and  $b_1 < 1$ . The predator  $Z$  and the prey  $X$  will coexist when  $a_3 > 1$ . The predator and  $Y$  will coexist when  $b_3 > 1$ .

Now we will begin examining systems of model 6.1. After examining models where both prey species supported the predator, it seems that there will always exist a point of coexistence for all three species can survive. Figure 6.1 is an example of a typical system. The system in this figure is

$$\begin{aligned}\frac{dX}{dt} &= X - .5XY - XZ - X^2 \\ \frac{dY}{dt} &= Y - .5XY - YZ - Y^2 \\ \frac{dZ}{dt} &= -Z + 2XZ + 2XY\end{aligned}$$

Next, let us examine systems where both competitors support the predator, but compete aggressively with each other. One system of this nature, graphed in figure 6.2, is

$$\begin{aligned}\frac{dX}{dt} &= X - 2XY - XZ - X^2 \\ \frac{dY}{dt} &= Y - 2XY - YZ - Y^2 \\ \frac{dZ}{dt} &= -Z + 2XZ + 2YZ\end{aligned}$$

From the figure it can be seen that the predator always survives and one of the competitors does not. A competitor either forces the other competitor into extinction or dies. In the figure the graphs of  $Z$  vs  $Y$  and time vs  $Y$  are given. The graphs of  $Z$  vs  $X$  and time vs  $X$  are identical to these.

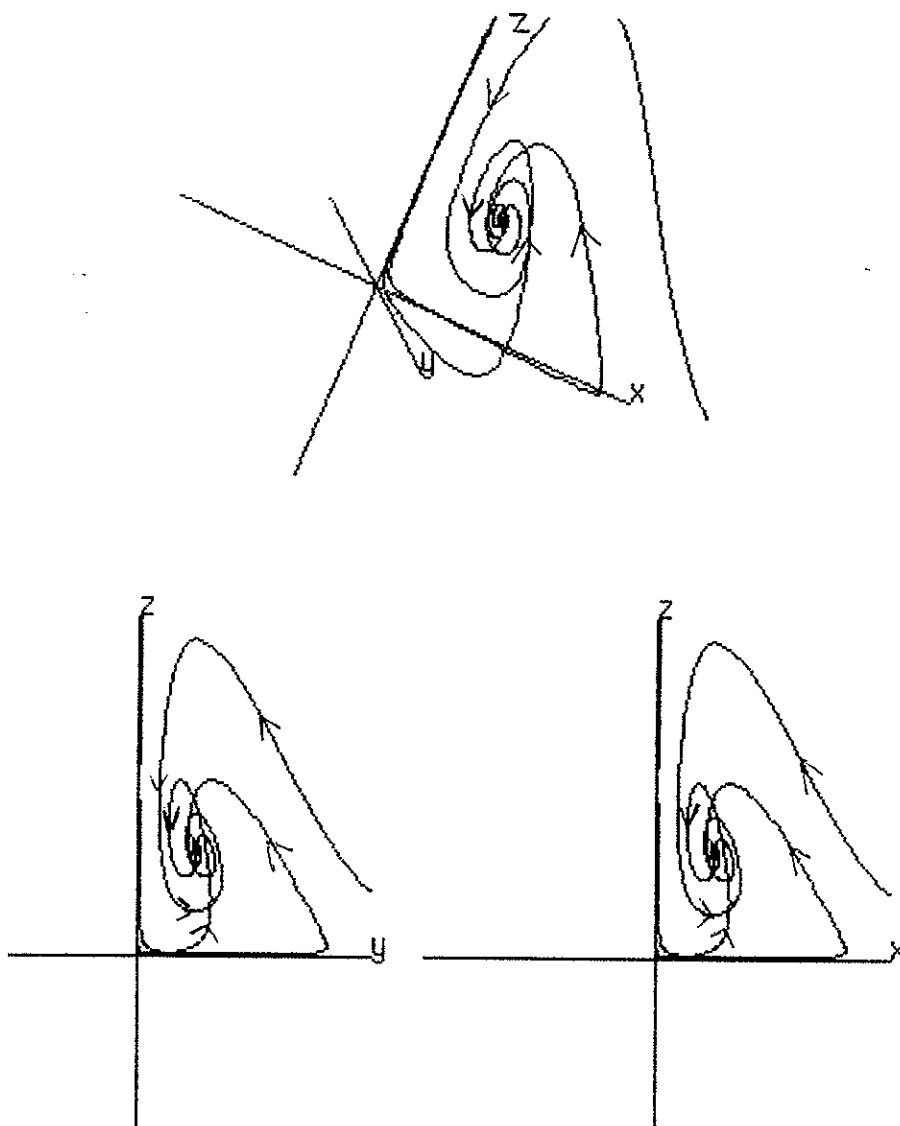


Figure 6.1: All three pairs coexist.

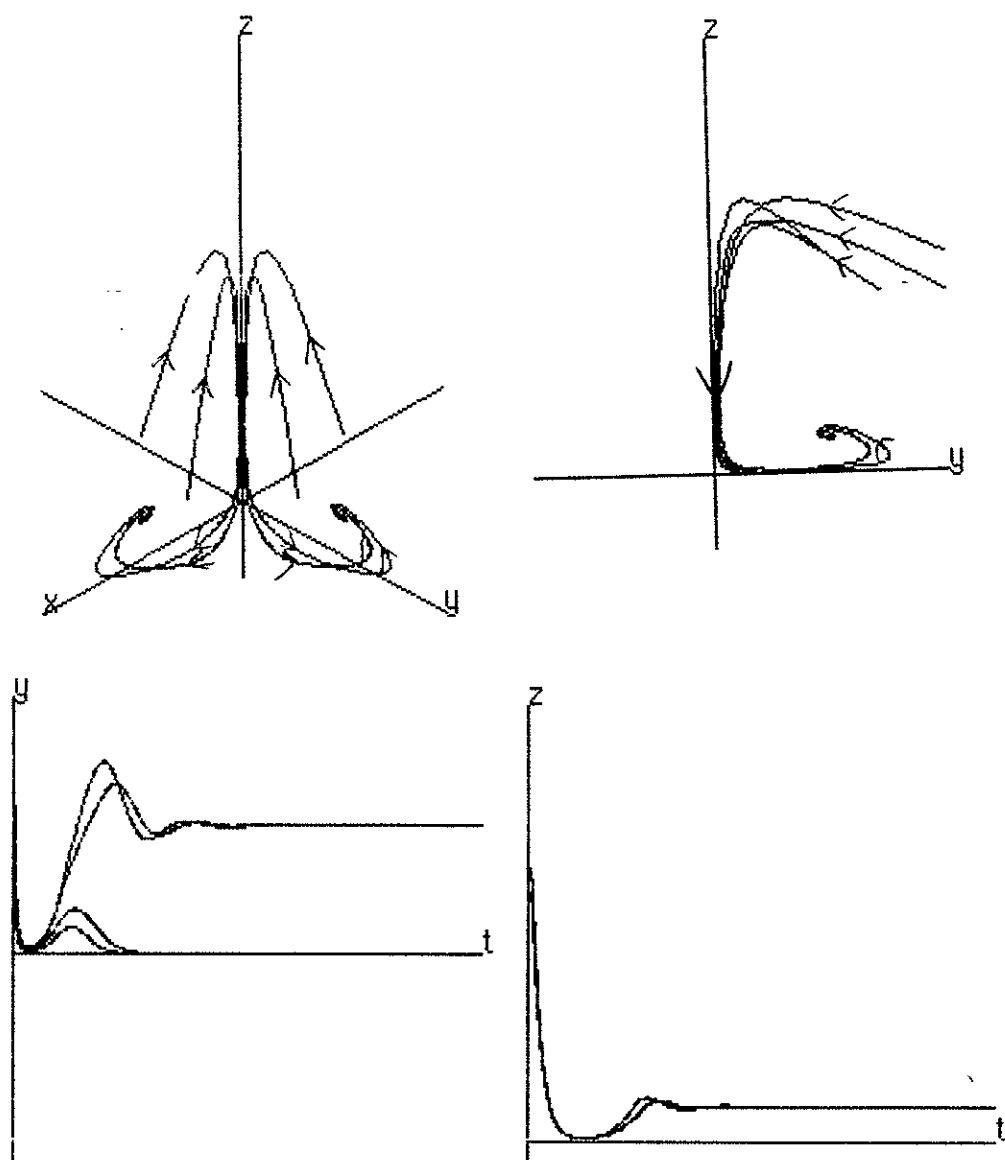


Figure 6.2: Aggressive competitors,  $X$  and  $Y$ , supporting the predator.

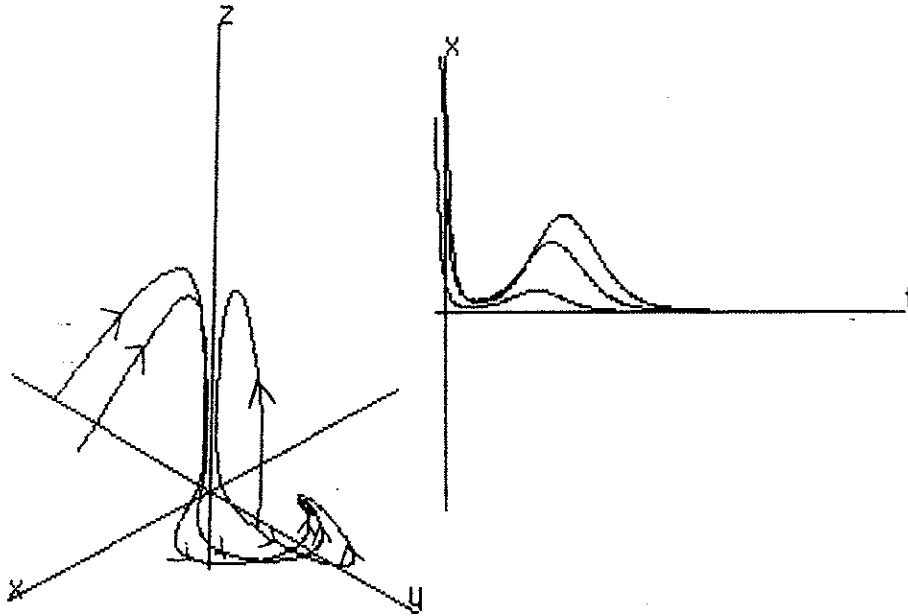


Figure 6.3: A dominant competitor  $Y$  supporting the predator  $Z$ .

Every example with two aggressive competitors had asymptotically stable equilibria where the competitors did not coexist.

Next, we look at systems where one competitor is competing aggressively with the other and both support the predator. In systems of this nature, one would expect the weak competitor to die, and the predator and remaining competitor to survive in a system like those of chapter four. This is exactly what the empirical evidence demonstrated. Consider the following system graphed in figure 6.3:

$$\begin{aligned}\frac{dX}{dt} &= X - 2XY - XZ - X^2 \\ \frac{dY}{dt} &= Y - .5XY - YX - Y^2 \\ \frac{dZ}{dt} &= -Z + 2XZ + 2YZ\end{aligned}$$

Clearly it seems that both the competitors will survive in system 6.1 only when they will coexist in the two species system. Now, we shall continue

this analysis by examining the parameters of the predator species.

If the predator is only supported by one competitor, and both competitors coexist, the system will have an asymptotically stable equilibrium where all three species coexist. A typical system of this nature is

$$\begin{aligned}\frac{dX}{dt} &= X - .5XY - XZ - X^2 \\ \frac{dY}{dt} &= Y - .5XY - YZ - Y^2 \\ \frac{dZ}{dt} &= -Z + .5XZ + 2YZ\end{aligned}$$

In this system, seen in figure 6.4, all three species coexist, but not in the elegant fashion of the other systems. This is shown in the graphs of  $X$  vs  $Z$  and  $X$  vs  $Y$ , where the trajectories twist and loop in more irregular patterns near the equilibrium.

Finally we examine the system where the predator cannot survive. By reducing the parameters in the predators equation, we create a system where neither prey species supports the predator. A typical system of this nature is

$$\begin{aligned}\frac{dX}{dt} &= X - .5XY - XZ - X^2 \\ \frac{dY}{dt} &= Y - .5XY - YZ - Y^2 \\ \frac{dZ}{dt} &= -Z + .5XZ + .5YZ\end{aligned}$$

In figure 6.5 it is clear that the predator dies and the competitors survive in a coexisting system following those of chapter two. The only thing interesting about this system is the rate the predator dies, which is very fast.

From the examples we have seen, it seems that the system 6.1 will only have an asymptotically stable equilibrium (or stable) when the conditions of the conjecture are met. At first, this seems reasonable, but there exists another possibility. If the predator is nearly supported by each of the competitors by themselves, could their combined support be enough? No examples could be found to support this intuition, but it is something that needs to be explored further.

Finally, it is time to develop and examine the last system in this work. In this system there are three levels. The first species,  $X$  forms the bottom

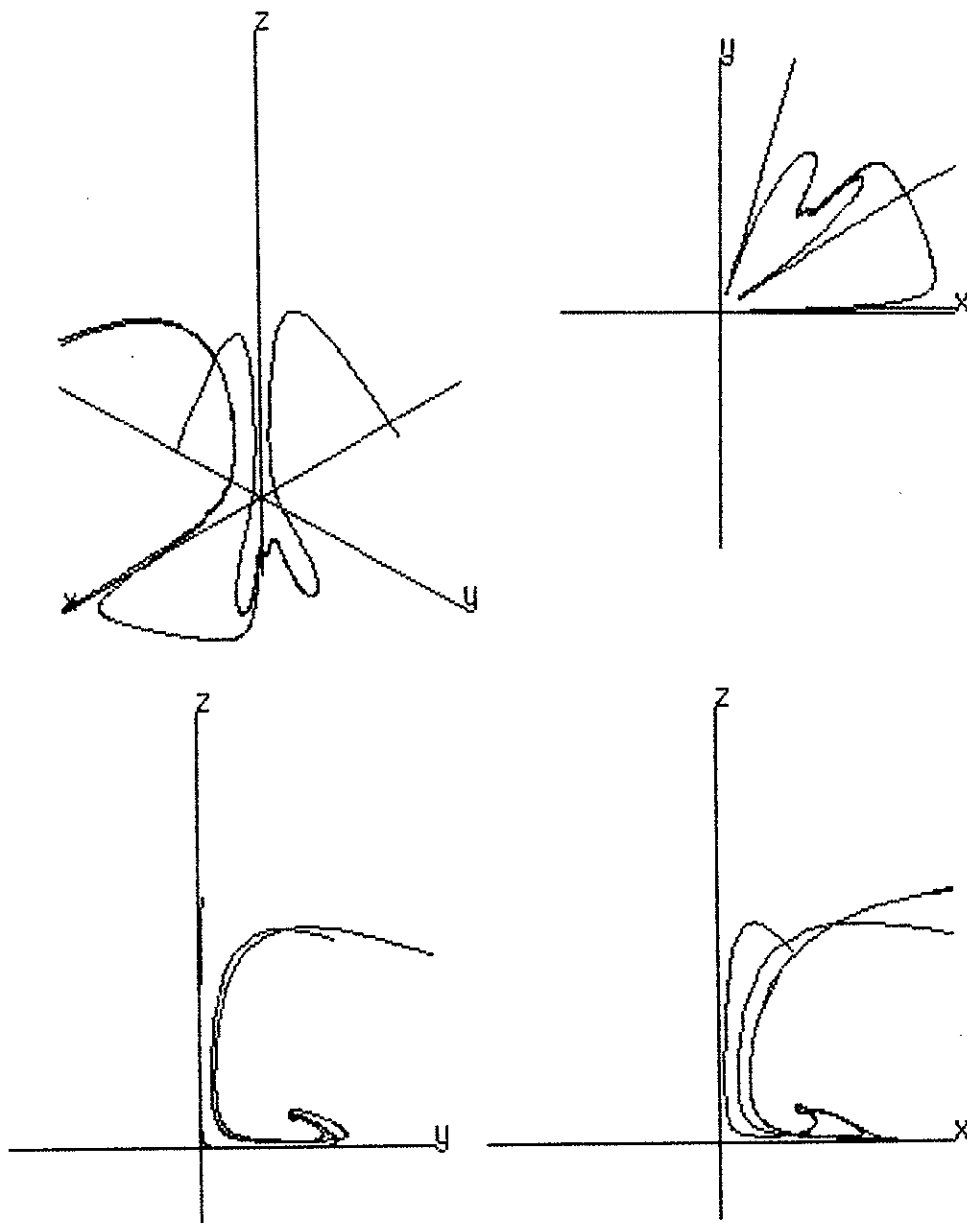


Figure 6.4: A predator only supported by one of two coexisting competitors.



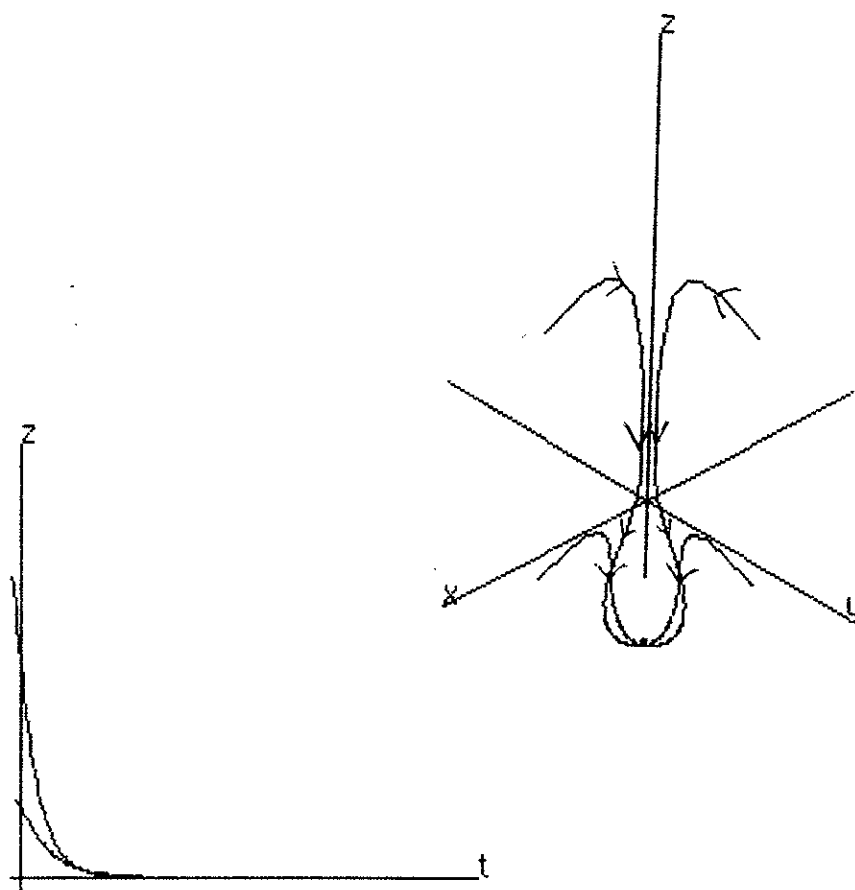


Figure 6.5: The unsupported predator becomes extinct.

level in this system. The second species,  $Y$ , is the middle level of the system preying on the bottom level. The  $Z$  species, forming the top level of this system, preys on the  $Y$  species alone and is preyed upon by no species.

If we make a few assumptions, we can construct a model for this system. The assumptions we make are:

1. In the absence of its predator the bottom level of the system,  $X$  follows a logistic model.
2. A prey species' growth rate is decreased by an amount proportional to the product of the prey and predator populations.
3. A predator species' growth rate is negative when no prey are present.
4. A predator species' growth rate is increased by an amount proportional to the product of the predator and prey populations.

The model we construct from the above assumptions about population behavior is:

$$\begin{aligned}\frac{dX}{dt} &= r_1X - b_1XY - p_1X^2 \\ \frac{dY}{dt} &= -r_2Y + a_2XY - c_2YZ \\ \frac{dZ}{dt} &= -r_3Z + b_3YZ\end{aligned}\tag{6.2}$$

There seems to be only one condition for this model to coexist. This condition follows from the interaction between the first two levels of the system,  $X$  and  $Y$ . All three species of this system will coexist if  $\frac{r_1}{p_1} > \frac{r_2}{a_2}$ . Note the growth rate equation of  $Z$  is exactly the predator equation from a Lotka-Volterra system. Recall the Lotka-Volterra system studied in chapter three. In that system there were no parameter limitations on the nature of the system, or to put it in simple terms, any two species fitting that model coexisted. In systems of this nature, as this one is, the population of the predator is determined by the parameters of the prey's growth rate equation.

An example of a coexisting system is

$$\begin{aligned}\frac{dX}{dt} &= X - XY - X^2 \\ \frac{dY}{dt} &= -Y + 5XY - YZ \\ \frac{dZ}{dt} &= -Z + 2XY\end{aligned}$$

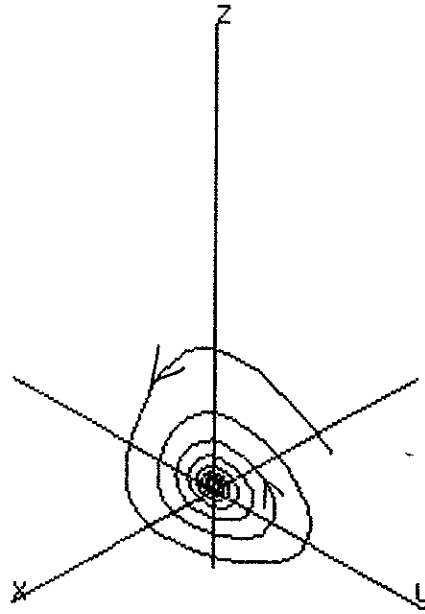


Figure 6.6: A coexisting three level system.

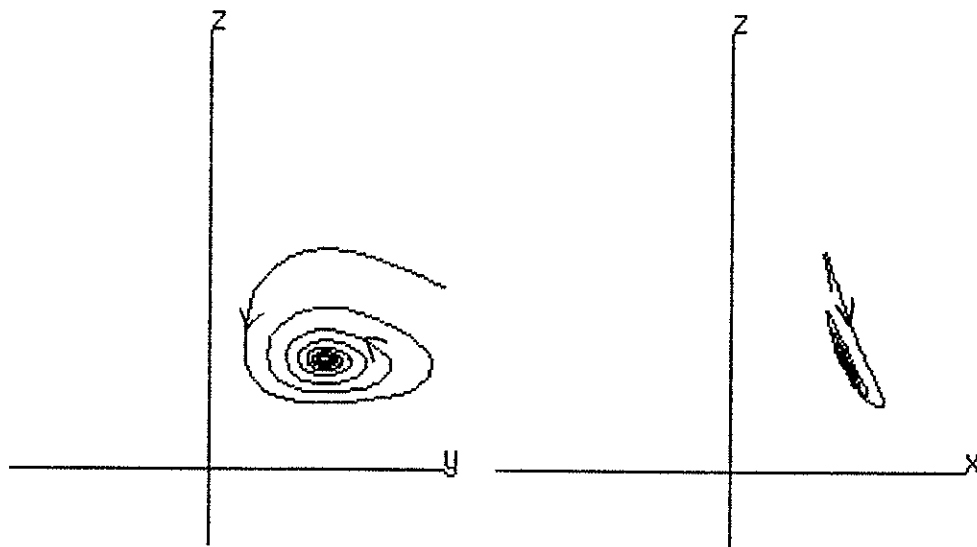


Figure 6.7: A couple more views of the coexisting three level system.

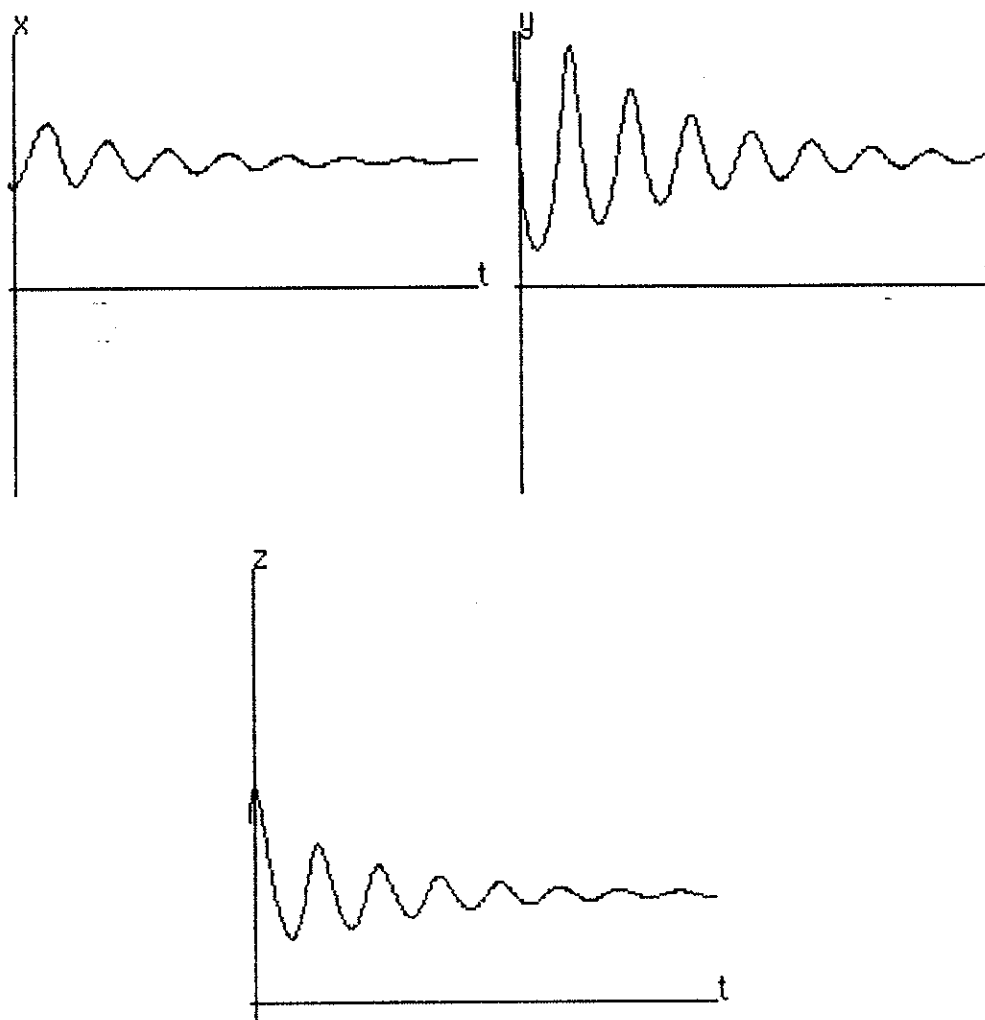


Figure 6.8: Each species over time  $t$ .

This system, shown in figures 6.6 through 6.8, coexists for all three species in a very elegant manner. The spiral effect from the modified Lotka-Volterra system between the species  $X$  and  $Y$  seems present. This first interaction, between  $X$  and  $Y$  is the damped cycle studied in chapter four. This cycle puts a restriction similar to a carrying capacity on the species  $Y$ . If the species  $Y$  does indeed have some carrying capacity laid upon it, then the second interaction between the  $Y$  and  $Z$  species is similar to a relationship like those of chapter four. Thus, both cycles are damped and the asymptotically stable equilibrium makes sense.

In this chapter, we have briefly looked at two different systems of closed hypothetical ecosystems. We have made conjectures that are supported by examples, but not proof. The next logical step in the process would be to examine the eigenvalues of the ecosystems at equilibria that are not too complicated. Unfortunately, because of time constraints this is not possible. Next, we shall turn to a more applied interpretation of this work.

## **Chapter 7**

# **Conclusions**

In this final chapter, we return to the difficulties encountered in chapter five. Also, we shall summarize the conjectures and theorems of this work and develop a conjecture about convexity. This final chapter is to serve as a springboard for continuing work on this subject.

Before we begin, let us compare the results of this work to some of the results of Robert May, whose work motivated parts of this study. May writes one must take "caution against any simple belief that increasing population stability is an automatic *mathematical* consequence of increasing multispecies complexity."<sup>1</sup> In this discussion about mathematical models, because it is the strong belief of this author, we will assume all the conjectures and theorems of this work are mathematically correct.

According to May, the idea that increasing complexity in ecosystems increases the probability of an ecosystem to coexist or balance is not true. However, May does not claim complexity reduces the probability of a system to coexist either. These are the two ideas of May I wish to address.

First, it would seem that May is correct. In the logistic model, all systems have a point of asymptotic stability. When we examined the competitive system of two species, we found a restriction on asymptotic stability in a three part inequality. After moving into systems of three species and examining the system of three competitors and the two level system, the requirements for coexistence of all species increased. The restrictions of the system of three competitors were three inequalities each having three parts. The restrictions on the two level system were one three part inequality and one two part inequality. Both of these are more complicated than any two species system we examined.

May is also correct to not argue complexity decreases the probability of a system to coexist. In all of the systems supporting May's claim in the paragraph above, there exists competition. Predator-prey systems do not seem to follow this example. The Lotka-Volterra system, because it consists of more species, is more complex than the logistic model. However, the Lotka-Volterra system has no parameter restrictions for stability either. Another example lies in comparing the modified Lotka-Volterra system to the three level predator-prey system in chapter six. Both of these systems have the same restrictions for asymptotic stability.

From the results of this work, it seems that increasing the number of competitive species in an ecosystem decreases the probability any random

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<sup>1</sup>May, Robert M. Stability and Complexity in Model Ecosystems. Princeton: Princeton University Press, 1973. pg 3.

ecosystem will coexist. At the same time, adding predators increases the complexity of the system without effecting the probability of a randomly generated system to have coexistence for all species.

This brings up an interesting question. If competition decreases the stability of a system and predators do not effect the stability, what is the impact of species that have symbiotic relationships on the stability of a system? This is a question this author would like to explore next.

Now let us return to chapter five. In particular, let us note the problem of chapter five. That is, in complicated systems at complicated equilibria determining the eigenvalues can be difficult. There may be another way to address this problem. We can break this determinant into several smaller subdeterminants. If we continue this process long enough, for any determinant we can find a series of four by four subdeterminants equivalent to this determinant. Each of these four by four subdeterminants compares the interaction between a pair of species in the system. Thus, by studying the system in pairs, it may be possible to determine the eigenvalues for the entire system at an equilibrium. This idea may help in studying complicated systems. However, it needs to be developed in greater detail first.

Now let us shift our perspective to just the competitive systems. For a system of two or three competitors, it seems that the systems with coexisting populations for all species have a certain convex set. This convex set is defined by the space or area enclosed within the segments of the isoclines from each species carrying capacity to the asymptotically stable equilibrium. This leads to a conjecture. This conjecture and the others of this work are given below.

*Conjectures:*

- For a system of competitors, if the set bounded by the segment of each isocline from its species' environmental carrying capacity to the equilibrium is convex or all species pairwise coexist, then that equilibrium is asymptotically stable.
- All three species of a hypothetical closed ecosystem following system 6.1 will coexist if the two prey species can coexist as a pair and either of the two prey species and the predator can coexist.
- All three species of a hypothetical closed ecosystem following system 6.2 will coexist if the species  $X$  and  $Y$  coexist.

Finally let us list the theorems developed in this work.



*Theorems:*

- The modified Lotka-Volterra system, system 4.1, will have an asymptotically stable equilibrium if  $\frac{r_1}{p} > \frac{r_2}{a_2}$ .
- For systems of three competitors with an equilibrium in the positive octant, if all trajectories must approach all isoplanes or have some equilibrium that is at least stable, and the system follows the model of system 5.2, then the equilibrium in the first octant is at least asymptotically stable.

In this analysis of mathematical systems modeling ecosystems, we examined several systems. However, there exist many more models than just those studied in this work. If we assume the only interactions between species are competition or predation, we can generate a list of possible ecosystems for three species. Also, for the list we are about to introduce, we shall assume each pair of species interacts. This will make systems with fewer interactions special cases of the ones we list. This list will be indexed by the number of competition interactions. Now, we leave you with this list.

*Three competitive interactions:*

- The system of three competitors studied in chapter five.

*Two competitive interactions:*

- Let  $X$  compete with  $Y$  and  $Y$  compete with  $Z$ , then there exists one interaction of predation. Without a loss of generality, let  $Z$  prey upon  $X$ .

*One competitive interaction:*

- The two level system of chapter six.
- Let  $X$  and  $Y$  compete with each other. The interactions of each competitor with  $Z$  must involve predation. Let  $X$  prey on  $Z$  and  $Z$  prey on  $Y$ .
- Let the competitors  $X$  and  $Y$  both prey on  $Z$ .

*No competitive interactions:*

- Since all interactions are predation, without a loss of generality we begin by assuming  $Y$  preys on  $X$ . Also, let  $X$  prey on  $Z$  and  $Z$  prey on  $Y$ . The three level system analyzed in chapter six is a special case of this model.

- Let  $Y$  prey on  $X$  and let  $Z$  prey on both  $X$  and  $Y$ .
- Let  $Y$  prey on  $X$  and let both  $X$  and  $Y$  prey on  $Z$ .

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